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"THE HEAD-CAPSULE
OF
COLEOPTERA

by

Fenner Satterwaith Stickney

THE HEAD-CAPSULE OF COLEOPTERA

BY

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I INTRODUCTION

LeConte and Horn published in 1883 a classification of the Coleoptera that has stood the wear of time remarkably well. Since then, however, a number of new classifications have been proposed: Lameere (1900 and 1903), Ganglbauer (1892-1904), Handlirsch (1906-1908), Kolbe (1901, 1908, and 1911), Sharp (1909), and Gahan (1911), all of which differ more or less seriously in one way or another, and show, for one thing, the need of further comparative morphological data, which is, of course, indispensable to the building of any thorough classification. Leng's recent catalogue (1920) also emphasizes this need.

A review of the literature seems to show but few studies based on the comparative morphology of a comprehensive series^{of} coleopterous families. A number of European workers have published comparative studies of the wings of Coleoptera, the most recent being by d'Orchymont (1920). Sharp and Muir (1912) and Muir (1918) have published the results of their investigations on the male genital tube in Coleoptera. Various internal structures have been discussed from time to time by a number of workers. Narrower in scope is the work of d'Orchymont (1918) on the classification of the Hydrophiloidea, based on a study of both the adult and the larva. Mulsop (1917), Böving and Champlain (1920), Craighead (1920), and Gage (1920), have published papers on the comparative morphology of various families, based on a study of the larvae. There are probably other comparative papers more or less extensive in scope, but I have not been able to find any such literature based on a study of the head-capsule. The comparative morphology of the head-capsule of some other orders,

however, has been investigated: Peterson (1915) on the Thysanoptera, Peterson (1916) on the Diptera, Yusa (1920) on the Orthoptera, and Hoke (1922) on the Plecoptera. These simply draw attention to the need of such an investigation of the head-capsule of Coleoptera.

With the broader vision in mind of a more satisfactory and natural classification of the Coleoptera, the following study on the comparative morphology of the head-capsule is offered. This study does not aim by any means to exhaust the subject. There have been too few species investigated in each family to justify the making of any sweeping statements. This study can simply point out characteristic conditions of structures as found in the different species of the families studied, revealing, therefore, inharmonies, and perhaps suggesting improvements on the present arrangement of the classification.

In order to reach a correct estimate of the degree of specialization of the various parts of the head-capsule, an hypothetical type, representing a supposed primitive condition, has been constructed. The structure of this hypothetical type is based on the structure of the head-capsule of generalized insects and of generalized adult and larval Coleoptera. Each structure has been treated separately, starting from the hypothetical type. The submentum has been included in this study because of its bearing on certain developmental processes. All statements made refer to the species listed under "materials" only. The material studied was soaked in a 10% solution of potassium hydroxide until clarified, then washed in distilled water to remove the hydroxide, and preserved in 70% alcohol. All dissections were made under a binocular microscope in 70%

alcohol in Syracuse watch glasses.

II. ACKNOWLEDGMENTS

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III. MATERIALS

An effort has been made to make this study as comprehensive as possible, including not only a wide series of families, but also a representation of the different subgroups within the families. Of the eighty-one families, exclusive of the Strepsiptera, listed by LeConte and Horn, representatives of all but one are listed in this study.

Leng in his recent catalogue lists one hundred and nine families. Of these ninety-four families have been studied representing one hundred and fifty-five species, of which one hundred and thirty have been figured. The fundamental structure of the head is, except in a few cases, practically similar for the two sexes. The sex has therefore been disregarded, except in the case of the brentid, *Eupsalis minuta*, the male of which has a long slender snout, as contrasted with the large broad snout of the female. The latter has been figured.

A number of attempts were made to arrange the figures in a linear series leading from the generalized to the specialized forms. All attempts proved unsatisfactory. No matter what structure or condition of a structure was used, the structure showed itself to be unstable within narrow limits and therefore could not be relied upon to illustrate a definite line of development. However, the meagre results obtained in trying to arrange the drawings in a linear series emphasized an important fact: that the various families of Coleoptera and even the subgroups within the families, have developed along many lines. For this study, the arrangement finally decided on, including the species, is that adopted by Leng. This arrangement will be valuable, in so far as the head-capsule is concerned, in showing the need for further morphological work towards the improvement of our classification of the Coleoptera. Owing to the number of drawings presented in this study it was deemed more practical to omit detailed descriptions. The salient features, only, of the various structures are discussed. The following list is arranged according to Leng's catalogue, and includes only those species studied:--

COLEOPTERA

Suborder Adephaga

Caraboidea.

1. Cicindelidae.

Megacephalini.-- *Tetracha carolina* (Figs. 2, 124, 248, 371)

Cicindelini.-- *Cicindela formosa* (Figs. 3, 125, 249, 372)

2. Carabidae.

Carabinae.-- *Calosoma calidum* (Figs. 4, 126, 250, 373)

Harpalinae.-- *Harpalus erraticus* (Figs. 6, 94, 129, 164, 251, 374)

Harpalus caliginosus

3. Amphizoidae.-- *Amphizoa lecontei* (Figs.)

4. Omophronidae.-- *Omophron americanum* (Figs. 5, 127, 252, 375)

5. Haliplidae.-- *Peltodytes 12-punctatus* (Figs. 7, 128, 253, 376)

6. Dytiscidae.

Colymbetinae.-- *Coptotomus longulus*

Dytiscinae.-- *Dytiscus hybrides*

Cybistrinae.-- *Cybister fimbriolatus* (Figs. 8, 130, 254, 377)

Gyrinoidea.

7. Gyrinidae.-- *Dineutes assimilis* (Figs. 9, 135, 255, 378)

Suborder Polyphaga

Hydrophiloidae.

8. Hydrophilidae.

Hydroscaphinae.-- *Hydroscapha natans* (Figs.)

Hydrophilinae.

Hydrophilini.-- *Hydrous triangularis* (Figs. 11, 131, 256, 379)

Hydrophilus obtusatus (Figs. 12, 132, 257, 380)

Silphoidea.

9. Platypsyllidae.-- *Platypsyllus castoris* (Figs.)

10. Leptinidae.-- *Leptinus testaceus* (Figs. 18, 133, 258, 381)

11. Silphidae.-- *Necrophorus carolina* (Figs. 13, 134, 259, 382)

12. Scydmaenidae.-- *Connophron fossiger* (Figs. 16, 136, 260, 383)

13. Orthoperidae.-- *Molamba lunata* (Figs. 10, 137, 261)

Staphylinioidea.

14. Staphylinidae.

Steninae.-- *Stenus flavicornis* (Figs. 19, 138, 262, 384)

Paederinae.-- *Gastrolobium bicolor* (Figs. 20, 139, 263, 385)

Staphylininae.-- *Creophilus villosus* (Figs. 14, 140, 264, 386)

Tachyporinae.-- *Tachinus fimbriatus* (Figs. 17, 141, 265, 387)

Aleocharinae.

Myrmedoniini.-- *Aleodorus bilobata*

Xenodusa cava

Aleocharini.-- *Aleochara lata* (Figs. 15, 142, 266, 388)

15. Pselaphidae.-- *Pilopius lacustris* (Figs.)

16. Ptilidae.-- *Limulodus paradoxus* (Figs. 21, 143, 267, 389)

17. Sphaeriidae.-- *Sphaerius politus* (Figs. 22, 144, 268, 390)

18. Scaphidiidae.-- *Scaphidium quadriguttatum* (Figs. 23, 145, 269, 391)

19. Histeridae.

Hololeptinae.-- *Hololepta fossularis*

Histrinae.-- *Hister merdarius* (Figs. 24, 147, 270, 392)

Saprinini.-- *Saprinus lugens*

Cantharoidea.

20. Lycidae.-- *Calopteron terminale* (Figs. 27, 149, 271, 393)

21. Lampyridae.

Lucidotini.-- *Lucidota corrusea*

Photini.-- *Photinus pyralis* (Figs. 28, 148, 272, 394)

22. Phengodidae.-- Phengodes plumosa (Figs. 29, 150, 273, 395)

23. Cantharidae.

Chauliognathini.-- Chauliognathus pennsylvanicus (Figs. 30, 146, 151)^{274, 396}

Cantharini.-- Podabrus rugulosus, Podabrus tomentosus,

Cantharis bilineatus (Fig. 275)

24. Melyridae.-- Collops nigriceps (Figs. 31, 152, 276, 397)

25. Cleridae.-- Trichodes nuttali (Figs. 32, 153, 277, 398)

26. Corynetidae.-- Necrobia rufipes (Figs. 33, 154, 278, 399)

Lymexyloidea.

27. Lymexylidae.-- Hylecoetus lugubris (Figs.)

28. Micromalthidae.-- Micromalthidae debilis (Figs.)

Cupesoidae.

29. Cupesidae.-- Cupes concolor (Figs. 36, 155, 279, 400)

Mordelloidea.

30. Cephaloidae.-- Cephaloon lepturides (Figs. 37, 156, 280, 401)

31. Oedemeridae.

Nacerdini.-- Nacerda melanura (Figs. 25, 157, 281, 402)

Asclerini.-- Asclera ruficollis

32. Mordellidae.-- Tomoxia bidentata (Figs. 38, 158, 282, 403)

33. Rhipiphoridae.-- Macrosiagon timidatum (Figs. 26, 159, 283, 404)

34. Meloidae.

Meloinae.-- Epicauta marginata (Figs. 34, 160, 284, 405)

Zonitinae.-- Zonitis atripennis

35. Eurystethidae.-- Eurystethus debilis (Figs. 39, 161, 285, 406)

36. Othniidae.-- Othnius sp. (Figs.)

37. Pythidae.-- Pytho americanus (Figs. 35, 163, 286, 407)

38. Pyrochroidae.-- Neopyrochroa flabellata (Figs. 40, 162, 287, 408)

39. Pedilidae.-- Macratris murina (Figs. 41, 165, 288, 409)

40. Anthicidae.-- *Notoxus anchora* (Figs. 42, 166, 290, 410)

Elateroidea.

41. Rhipiceridae.-- *Sandalus niger* (Figs. 43, 167, 289, 411)

42. Elateridae.

Pyrophorinae.-- *Alaus oculatus* (Figs. 44, 169, 291, 412)

Elaterinae.-- *Melanotus communis*

Cardiophorinae.-- *Cardiophorus gagates*

43. Eucnemidae.-- *Tharops ruficornis* (Figs. 46, 170, 292, 413)

44. Throscidae.-- *Throscus chevrolati* (Figs. 45, 168, 293, 414)

45. Buprestidae.

Polycestini.-- *Acmaeodera pulchella*

Chalcophorini.-- *Chalcophora virginiensis* (Figs. 47, 172, 294, 415)

Buprestini.-- *Dicerca divaricata*

Chrysobothrini.-- *Chrysobothris femorata*

Agrilini.-- *Agrilus ruficollis*

Dryopoidea.

46. Psephenidae.-- *Psephenus lecontei* (Figs. 48, 174, 295, 416)

47. Dryopidae.-- *Helichus striatus* (Figs. 49, 175, 296, 417)

48. Elmidae.-- *Stenelmis sinuata* (Figs. 52, 176, 297, 418)

49. Heteroceridae.-- *Heterocerus undatus* (Figs. 53, 171, 298, 419)

50. Georyssidae.-- *Georyssus californicus* (Figs. 54, 173, 299, 420)

Dascilloidea.

51. Eucinetidae.-- *Eucinetus morio* (Figs. 50, 177, 300, 421)

52. Cyphonidae.-- *Cyphon ruficollis* (Figs. 51, 178, 301, 422)

Byrrhoidea.

53. Dermestidae.-- *Dermestes lardarius* (Figs. 55, 179, 302, 423)

54. Byrrhidae.-- *Byrrhus americanus* (Figs. 56, 180, 303, 424)

55. Nosodendridae.-- *Nosodendron unicolor* (Figs. 57, 181, 304, 425)

Rhysodoidea.

56. Rhysodidae.-- *Rhysodes americanus* (Figs. 58, 182, 305, 426)

Cucujoidea.

57. Ostomidae.-- *Tenebroides sinuatus* (Figs. 59, 183, 306, 427)

58. Nitidulidae.--

Nitidulinae.-- *Phenolia grossa* (Figs. 60, 184, 307, 428)

Cryptarchinae.-- *Glischrochilus quadriguttatus* (Figs. 61, 185, 308, 429)

59. Monotomidae.-- *Phyconomus marinus* (Figs. 63, 186, 309, 430)

60. Cucujidae.

Cucujini.-- *Cucujus clavipes* (Figs. 62, 187, 310, 431)

Telephanini.-- *Telephanus velox*

61. Erotylidae.

Langurinae.-- *Languria mozardi* (Figs. 64, 188, 311, 432)

Erotylinae.

Triplacini.-- *Tritoma angulatus*

Dacnini.-- *Megalodacne fasciata* (Figs. 65, 189, 312, 433)

62. Derodontidae.-- *Derodontus maculatus* (Figs. 66, 193, 313, 434)

63. Cryptophagidae.-- *Anchicera ephippiata* (Figs. 67, 190, 314, 435)

64. Byturidae.-- *Byturus unicolor* (Figs. 68, 191, 315, 436)

65. Mycetophagidae.-- *Mycetophagus punctatus* (Figs. 69, 192, 316, 437)

66. Colydiidae.-- *Philothermus glabriculus* (Figs. 70, 194, 317, 438)

67. Lathridiidae.-- *Melanophthalma angularis* (Figs. 74, 195, 318, 439)

68. Mycetidae.-- *Phymaphora pulchella* (Figs. 71, 196, 319, 440)

69. Endomychidae.-- *Endomychus biguttatus* (Figs. 75, 197, 320, 441)

70. Phalacridae.-- *Phalacrus politus* (Figs. 72, 198, 321, 442)

71. Coccinellidae.

Coccinellini.-- *Hippodamia convergens* (Figs. 76, 199, 322, 443)

Adalia bi-punctata (Figs. 79, 200, 323, 444)

Anatis 15-punctata

Chilocorini.-- *Chilocorus bivulnerus*

Tenebrionoidea.

72. Alleculidae.-- *Pseudocistela brevis* (Figs. 78, 201, 324, 445)

73. Tenebrionidae.

Tenebrioninae.-- *Alobates pennsylvanica* (Figs. 73, 202, 325, 446)

Tenebrio molitor (Figs. 80, 203, 326, 447)

Boros unicolor (Figs. 81, 204, 327, 448)

Diaperinae.-- *Diaperis maculata*

74. Lagriidae.-- *Arthromacra aenea* (Figs. 77, 205, 328, 449)

75. Monommidae.-- *Hyporhagus* sp. (Figs. 82, 206, 329, 450)

76. Melandryidae.-- *Penthe obliquata* (Figs. 83, 207, 330, 451)

Bostrichoidea.

77. Ptinidae.-- *Ptinus brunneus* (Figs. 84, 208, 331, 452)

78. Anobiidae.-- *Sitodrepa panicea* (Figs. 85, 209, 332, 453)

79. Bostrichidae.-- *Bostrichus bicornis* (Figs. 86, 211, 333, 454)

80. Lyctidae.-- *Lyctus planicollis* (Figs. 87, 210, 334, 455)

81. Sphindidae.-- *Sphindus americanus* (Figs. 89, 212, 335, 456)

82. Cisidae.-- *Flesiocis cribrum* (Figs. 88, 213, 336, 457)

Scarabaeoidea.

83. Scarabaeidae.

Aphodiinae.-- *Aphodius fimetarius* (Figs. 90, 214, 337, 458)

Melolonthinae.-- *Dichelonyx elongata* (Figs. 91, 215, 338, 459)

Rutelinae.-- *Pelidnota punctata* (Figs. 92, 216, 339, 460)

Dynastinae.-- *Strategus julianus* (Figs. 93, 217, 340, 461)

Cetoniinae.-- *Osmoderma eremicola* (Figs. 95, 218, 341, 462)

84. Trogidae.-- *Trox suberosus* (Figs. 96, 219, 342, 463)

85. Lucanidae.-- *Pseudolucanus dama* (Figs. 97, 220, 343, 464)

86. Passalidae.-- *Passalus cornuta* (Figs. 98, 221, 344, 465, 466)

Cerambycoidea.

87. Cerambycidae.

Prioninae.

Parandrinini.-- *Parandra brunnea* (Figs. 105, 222, 345, 467)

Prionini.-- *Derobrachus brunneus* (Figs. 100, 223, 346, 468)

Cerambycinae.-- *Glycobius speciosus* (Figs. 101, 224, 347, 469)

Lamiinae.-- *Tetraopes tetraophthalmus* (Figs. 102, 225, 348, 470)

88. Chrysomelidae.

Donaciinae.-- *Donacia piscatrix* (Figs. 103, 226, 349, 471)

Orsodacninae.-- *Syneta ferruginea* (Figs. 99, 227, 350, 472)

Criocerinae.-- *Crioceris asparagi* (Figs. 104, 228, 351, 473)

Cryptocephalinae.-- *Cryptocephalus quadruplex* (Figs. 106, 229, 352, 474)

Eumolpinae.-- *Chrysochus auratus* (Figs. 107, 230, 353, 476)

Chrysomelinae.-- *Leptinotarsa decimlineata* (Figs. 108, 231, 354, 477)

Galerucinae.-- *Diabrotica 12-punctata* (Figs. 114, 231, 355, 478)

Malticinae.-- *Blepharida rhois* (Figs. 110, 233, 356, 475)

Hispinae.-- *Anoplitis nervosa* (Figs. 111, 234, 357, 479)

Cassidinae.-- *Chelymorpha argus* (Figs. 112, 235, 358, 481)

89. Mylabridae.-- *Eachymerus arthriticus* (Figs. 113, 236, 359, 480)

Mylabris obtectus

Brentoidea.

90. Brentidae.-- *Eupsalis minuta* (Figs. 109, 237, 360, 482)

Curculionoidea.

91. Belidae.-- *Ithycerus noveboracensis*

92. Platystomiidae.-- *Eurymycter fasciatus* (Figs. 115, 238, 361, 483)

93. Curculionidae.

Rhynchitinae.-- *Rhynchites bicolor* (Figs. 117, 239, 362, 484)

Attelabinae.-- Attelabus analis (Figs. 120, 240, 363, 485)

Allocorhyninae.-- Allocorhynus slossoni (Figs.)

Otiiorhynchinae.-- Epicaerus nubricatus (Figs. 116, 241, 364, 486)

Curculioninae.-- Lixus mscer (Figs. 123, 242, 366, 488)

Thecesterinae.-- Thecesterus humeralis (Figs. 119, 243, 367, 487)

Calendrinae.-- Sphenophorus aequalis (Figs. 121, 244, 368, 489)

Scolytoidea.

94. Scolytidae.

Scolytinae.-- Scolytus quadrispinosus (Figs. 122, 245, 365, 490)

Hylesininae.-- Dendroctonus valens (Figs. 118, 246, 369, 491)

IV. HEAD-CAPSULE.

There exists a distinct homogeneity in the general character of the structure of the head-capsule of Coleoptera. Its uniform strong chitinization is typical. So is the spacious area occupied by the mouth-parts, producing a relatively broad cephalic end. Especially characteristic is the wide space between the occipital foramen and the submentum. Then, there is that indescribable similarity of structure, even between groups widely separated, that can best be appreciated from a thorough knowledge of the morphology. As an illustration, there is little superficial resemblance between Harpalus (Figs. 625, 374) and Phalacrus (Figs. 32, 321, 448), either in external or internal morphology. Their distinct differences are merely due to two divergent lines of development. The structures of the dorsal surface of Phalacrus have become highly specialized, whereas those of Harpalus are relatively generalized. On the other hand, on the ventral surface the metatentorium has remained in a relatively primitive condition in Phalacrus, whereas in Harpalus its position is highly specialized. The internal structures of Phalacrus are rudimentary or lack-

ing, while in *Harpalus* they are in a well-developed primitive state. Considering the degree of generalization of each species, there can hardly be any question that *Harpalus* is the more generalized. The above comparative description simply illustrates roughly the problems of complexity of development that are encountered. The two distinctive kinds of development as shown above for *Harpalus* and *Phalacrus*, that of specialization of the dorsal surface and that of separate specialization of the ventral surface, do not in the least necessarily parallel one another in the Coleoptera. Indeed, these two lines of development are predominantly divergent. In the majority of species, the development is trending towards the obliteration of sutures and consequent consolidation of sclerites, and towards the development of a compactness of form of the sclerites that do not consolidate. The general trend towards a cephalization of migratory structures is a part of this process, too, as well as the development of a stronger chitinization of the head-capsule as a whole. The entire phenomenon appears to be for purposes of strengthening the head. Besides *Phalacrus* typical examples are *Tenebroides* (Fig. 59), *Glischrochilus* (Fig. 61), *Megalodacne* (Fig. 65), and all the *Scarabaeoidea*. On the other hand these processes have lagged behind on the ventral surface in *Phalacrus* and others. It is true that the hypothetical type (Fig. 247) shows a marked cephalization of the submentum, with obliteration of sutures resulting from this migration. Yet the predominant condition of the heads studied shows only a certain degree of removal from the primitive type. Stronger chitinization has probably kept pace with the cephalization of the dorsal surface, as well as the growing compactness of such a structure as the submentum. But the very significant structure of the ventral surface, the meta-

ina, only shows a certain degree of removal from the primitive condition in most of the heads.

Developmental processes such as are discussed above can be best worked out through a comparative study of a large series of forms. In fact the determination of the homologies of some structures entering into these developmental processes, as for example the various changes in the epicranial suture, and the determination of the nature and line of development of the area between the occipital foramen and the submentum, would probably be most difficult without this comparative study. The chief value of this study lies in all probability in the determination of homologies, to the end of understanding the lines of development present. The homology existing between the various structures of the head-capsule of Coleoptera and other orders of insects, particularly the generalized orders, seems to work out satisfactorily. From such an homology the hypothetical type was constructed without much difficulty. In general appearance it is oblong and rather flattened dorso-ventrally. Such a form is fairly characteristic of generalized insects and of the more generalized Coleoptera. The mouth may be considered as directed cephalad. Such a direction is representative of the vast majority of the heads, and for purposes of convenience, at least, the following discussion considers the head as extending cephalad. Some possible exceptions in which the head appears to be directed ventrad are found in Calopteron (Fig. 149), Macrosciagon (Fig. 159), Tharops (Fig. 170), Throscus (Fig. 168), Byrrhus (Fig. 180), and a few others. It should not be forgotten, however, that in primitive insects the mouth is directed ventrad, and the occipital foremen is on one side instead of at the opposite end.

Epicranial suture.-- The line of closure of the head in the em-

bryo is represented by the epicranial suture. The complete epicranial suture is typical of generalized insects. Where it is present in Coleoptera, this denotes a generalized condition. The primitive form of the epicranial suture is that of a deep inverted Y, with the cephalic ends of the arms near the lateral border of the labrum. The hypothetical head is represented as having a complete epicranial suture. The epicranial stem extends to a transverse line drawn through the middle of the compound eyes. Branching here, the epicranial arms continue to the margin of the head cephalad of the compound eyes. A complete epicranial suture is not of general occurrence in the Coleoptera. It is practically complete in Hydrous (Fig. 11) and Hydrophilus (Fig. 12), very distinct and sharply invaginated in both, particularly so in the former, and characteristic in form. Each arm reaches the margin of the head almost immediately cephalad of a compound eye, and the arms are not as generalized in position as they are in *Epicaura* (Fig. 34), where they are quite distinct. The only other occurrence of a complete epicranial suture is in Chelymophra (Fig. 112). Here the arms meet the stem farther caudad than in the other genera named. The arms in this last genus are distinctly curved, as contrasted with the more or less straight arms in the above-mentioned genera.

The epicranial arms or some portion of them are present in all Coleoptera, except possibly in Calopteron (Fig. 27) and Photinus (Fig. 28). One or more species of every superfamily of the Adephaga and Polyphaga, except the Elateroidea, Byrrhoidea, Rhysodoides, and Rhynchophora, have the arms complete. In the Caraboidea they are prominent as nearly straight sutures across the head, as in Tetracha (Fig. 2), Cicindela (Fig. 3), Calosoma (Fig. 4), and Harpalus (Fig. 6). Their most generalized condition in the Adephaga is found in Omophron (Fig. 5).

in which they extend from the meson at a sharp angle. Representative species of other superfamilies that have the arms complete are: *Necrophorus* (Fig. 13), *Tachinus* (Fig. 17), *Chauliognathus* (Fig. 30), *Cupes* (Fig. 36), *Cephaloon* (Fig. 37), *Notoxus* (Fig. 42), *Heterocerus* (Fig. 53), *Eucinetus* (Fig. 50), *Mycetophagus* (Fig. 69), *Tenebrio* (Fig. 80), *Bostri-chus* (Fig. 86), *Aphodius*. (Fig. 90), and nearly all the *Cerambycoidea*. Species having parts of the epicranial stem preserved are not very common. In *Omophron* (Fig. 5), *Tachinus* (Fig. 17), *Penthe* (Fig. 83), and a number of the *Cerambycoidea*, parts of the cephalic end can be identified; in *Omophron* (Fig. 5), *Phengodes* (Fig. 29), *Cupes* (Fig. 36), *Sitodrepa* (Fig. 85), *Blepharida* (Fig. 110), and a number of the *Rhynchophora*, parts of the caudal end are present. *Chalcophora* (Fig. 47) *Tetraopes* (Fig. 102) are peculiar in possessing practically all of the stem but little of the arms. The arms in *Chalcophora* are as short as in any other species studied. Parts of the arms are present in every degree of length from nearly meeting on the meson, as in *Nosodendron* (Fig. 57), to almost complete disappearance as in *Chalcophora* (Fig. 294) and *Rhysodes* (Fig. 182). They also show varying degrees of disappearance and invagination, from the deep, distinct invaginations of such forms as *Dineutes* (Fig. 9), *Necrophorus* (Fig. 13), *Tachinus* (Fig. 17), *Heterocerus* (Fig. 53), and *Arthromacra* (Fig. 77), to the faint or slender and shallow or not at all invaginated sutures characteristic of the *Scarabaeoidea*. The character of the invagination associated with the epicranial arms is not as simple as may be thought. In *Harpalus* (Figs. 694, 164), the epicranial arms extend from the meson along the edge of the invagination to the pretentorialae, from which they extend to the bottom of the invagination, curve laterad, and continue to the margin of the head. The course of the epicranial arms can be better

understood from *Omophron* (Fig. 5), a related genus, which has retained the cephalic portion of the epicranial stem. The line of the invagination appears to be and often is considered to be simply the clypeal suture. If a specimen of *Harpalus* is soaked for a long time in potassium hydroxide the invagination can be opened and the various structures in this region studied advantageously. The invagination when opened (Fig. 164) will be seen to assume a deep wide wedge-shaped form, extending entirely across the dorsal surface of the head. The pretentorinae are located on the external dorsal surface just caudad of the cephalic margin of the invagination. Although the epicranial arms are not in evidence anywhere between the meson and the pretentorinae, it is assumed that the cephalic marginal ridge must represent them, since the pretentorinae are not only located caudad of the invagination, but the arms are quite distinct, extending from the pretentorinae to the bottom of the invagination, in which they then curve laterad and continue to the margin of the head. From a cross-section (Fig. 94) it will be seen that the pretentorium expands cephalad in characteristic form from the pretentorina along the epicranial arm to the bottom of the invagination. In *Calosoma* (Fig. 4) the same condition of this region is found as in *Harpalus*. In *Omophron* (Fig. 5) the epicranial arms are distinct between the pretentorinae, extending from the meson along the cephalic border of the invagination. From figure 164 it will be observed that the cephalic border of the invagination in *Harpalus* is along the imaginary line of the fronto-clypeal suture. This border may represent the cephalic limit of the front. The invagination, then, in *Harpalus* and *Calosoma* includes the entire front. The line of the invagination instead of being solely a part of the epicranial suture is in fact

compound in nature, representing the approximation of the caudal borders of the front and post-clypeus, and that part of it between the pretentorinae may be termed the clypeofrons. Laterad of the pretentorinae to the margin of the head the line of the invagination is readily seen to be an approximation of a part of the vertex with the caudal border of the postclypeus and cannot be included in the clypeofrons. Due to the more primitive position of the epicranial arms in *Omophron* the invagination in this genus contains only a part of the front, hence the line of the invagination between the pretentorinae is simple in nature. In *Tachinus* (Fig. 17) the epicranial stem extends distinctly into the invagination, the arms continuing in the same to the margin of the head. As should be expected, the pretentorinae are within the invagination. The line of the invagination in *Tachinus* is then of a different character from that of either *Harpalus* or *Omophron*. In *Tachinus*, it has nothing whatever to do with the epicranial suture nor with any other suture, being throughout the approximation of parts of the external dorsal surface of the vertex and the front. It is obvious from the above discussion of three types of the invagination associated with the epicranial arms that the dorsal surface of the head-capsule in Coleoptera must be studied most carefully before a correct interpretation of the parts can be made. This is most true in the case of any invagination that may be present. The latter may not be readily observed when the head-wall is strongly and darkly chitinized, necessitating treatment of such specimens before the parts can be clearly made out. In some genera such as *Dermestes* (Fig. 55), *Scolytus* (Fig. 121), and *Dendroctonus* (Fig. 118) all external trace of the line of the invagination may be lost. In such cases a true understanding of the parts can only be gained

from an examination of the ental surface of the head. But in specialized forms the ental indication of the invagination may also be effaced.

The epicranial suture can always be located from the determination of the position of the pretentorina. The latter is always closely associated with the epicranial suture, being present either in or just off of the suture, in which case the pretentorina resembles a sort of pocket. There is usually little difficulty experienced in locating the suture. The cephalic ends of the arms are the most persistent parts of it, being present when the remainder of the suture cannot be identified. Interesting examples are found in most Rynchophora, where the remnants of the epicranial arms are represented by short furrows located at the cephalic and of the snout. The epicranial arms are typically structures of the dorsal aspect, but with the shifting and modification of other parts of the head may be confined to the lateral aspect as in *Dineutes* (Fig. 175), *Helichus* (Fig. 175), *Adalia* (Fig. 200), or to the ventral aspect as in *Cybister* (Fig. 259), *Hydrous* (Fig. 256), and *Phalacrus* (Fig. 324).

Vertex.-- That part of the head-capsule not embraced by the three primary sclerites cephalad of the epicranial arms, the occiput, and the postgena, constitutes the vertex. Its extent is determined by the form and size of the three above-mentioned areas. For instance, in those species with much reduced epicranial arms, as in *Creophilus* (Fig. 14), *Limulodes* (Fig. 21), *Adalia* (Fig. 79), and *Phalacrus* (Fig. 72), the extent of the vertex is correspondingly increased. In the Rynchophora, as represented by such species as *Ilixus* (Fig. 123) and *Sphenophorus* (Fig. 121), it is very extensive, including practically all of the snout of the dorsal and lateral surfaces. The area

located on the lateral aspect cephalad of the compound eyes, between the latter and the epicranial suture, is the gena, a part of the vertex. The limits of the gena are not definite. The prominent ridge in many genera, dorso-mesad of each gena and antecoria, is the so-called frontal ridge, that extends in the general direction from the epicranial arms to the mesal margin of the compound eyes. The frontal ridge is prominent in *Harpalus* (Fig. 6), *Necrophorus* (Fig. 13), *Trichodes* (Fig. 32), *Pyrochroa* (Fig. 40), *Dermestes* (Fig. 55), and many others.

Occipital Suture.-- In generalized insects the occipital suture is confined to the ventral or caudal aspect, beginning near the lateral margin of the postcoila and extending around the caudal or dorsal margin of the occipital foramen. In the Coleoptera this suture arises laterad of the postcoila, extends cephalad for a considerable distance, then curves abruptly laterad, extending onto the dorsal aspect of the head, where it joins the suture of the other side at the meson. The genus *Cicindela* possesses the most generalized condition of this suture found in the Coleoptera. The cephalic end of the suture is modified into a ridge. This ridge is considered a later development, and is not shown in the hypothetical type. It unquestionably represents a part of the occipital suture, and can be identified in practically all the Coleoptera, as in such widely separated groups as *Molamba* (Fig. 26), *Nacerda* (Fig. 28), and *Byturus* (Fig. 35). The occipital suture separates the vertex from the occiput and the postgena. Only the Caraboidea seem to possess with certainty an unmodified occipital suture. In *Cicindela* (Fig. 3) it is complete, and nearly so in *Tetrache* (Fig. 2) but very faint in great part. In *Calosoma* (Fig. 25) the unmodified suture begins farther caudad and is more distinct.

In *Omophron* (Fig. 127) two short, characteristically curved, lateral ridges no doubt represent remnants of the occipital suture. The ridge across the lateral aspect in *Peltodytes* (Fig. 128) may also represent this suture. In *Cybister* (Fig. 254) it is probably represented by the crescent-shaped suture on the ventral aspect. Ridges or furrows appearing in the same general location in other species, such as *Aleochara* (Fig. 266), *Throscus* (Fig. 293), *Cyphon* (Fig. 301), and *Aphodius* (Fig. 337), may possibly be homologized as occipital sutures. In most cases these ridges seem to be merely to mark the limits to which the head is telescoped in the prothorax.

Occiput.-- In those species possessing an occipital suture the occiput is recognized as a distinct area. It includes the region between the occipital foramen and the occipital suture as far as the postgena, appearing as a sort of broad band across the dorsal aspect, divided by the epicranial stem and indistinguishably fused on the lateral aspect with the postgenae. Examples of a well-marked occiput are present in *Tetracha* (Fig. 2), *Cicindela* (Fig. 3), *Calosoma* (Fig. 4), and *Earpalus* (Fig. 6). In *Omophron* (Fig. 127) the occipital suture is so short that the limits of the occiput cannot be definitely determined. In those species not possessing a recognizable unmodified portion of the occipital suture, the limits of the occiput can only be judged accordingly. Even in generalized insects the occiput is nearly always fused with the postgenae, and is so represented in the hypothetical type.

Compound Eyes.---There is a great similarity in the form and location of the compound eyes. The general form is oval. They are located near the middle of the lateral margin of the head. Such a form and location is given in the hypothetical type. There are a number

of interesting variations in form from the normal type. *Dineutes* (Fig. 135) and *Tetraopes* (Fig. 102) have four complete eyes. This phenomenon is produced by a projection of part of the vertex into the eye that in time completely separates the two halves. The line of closure between the projection and the opposite side is indicated by a distinct line--the exoculata. The beginning of such a projection is shown in *Cephaloon* (Fig. 156), *Epicanta* (Fig. 160) and many others. In *Cistela* (Fig. 201) and *Osmoderna* (Fig. 218) the projection extends more than half-way across the eye. In *Throscus* (Fig. 168) the projection nearly separates the two halves. The eyes of *Peltothytes* (Fig. 7) *Photinus* (Fig. 28) and *Stenus* (Fig. 19) are very large. Unusual forms of the eyes are found in *Hypophagus* (Fig. 82), where they are very long and narrow, nearly meeting on the dorso-meson; in *Cryptocephalus* (Fig. 106), where they are prominent, crescent-shaped, and extend well caudad on the dorsal surface; and in *Aphodius* (Fig. 90), where they are relatively small and square-like. The eyes of *Limulodes* (Fig. 143) are transparent and almost invisible; those of *Leptinus* (Fig. 133) are completely wanting.

Oculata.-- The oculata is present only on the inside periphery of the eye as a broad ring-like shelf. It is considered of little importance in this study. Its general size is indicated by the dotted area within the eyes of *Cicindela* (Fig. 125), *Dineutes* (Fig. 135), *Passalus* (Fig. 221), and a few others. In forms with divided eyes the two sides of an oculata are pressed together forming an exoculata.

Supratentorina.-- The supratentorinae represent the point of attachment on the head-capsule of the supratentorium. They are not thought to be primary invaginations and may probably represent no more than depressions. In the Coleoptera the supratentorinae are not

prominent, as the pretentorinae and metatentorinae often are. They are situated on the dorsal surface of the vertex. Their presence is not general, occurring commonly only in the Staphylinidae. Outside of this superfamily the supratentorinae are found only in *Ethyconomus* (Fig. 63) and *Philothermus* (Fig. 70). The supratentoria are usually attached to the inner membrane of the body-wall, but unless an actual mark of their presence is indicated on the external surface the supratentorinae are not considered as present. In generalized insects the latter are generally present. Their presence in the Coleoptera should indicate a primitive state.

Ocelli.-- In all the Coleoptera examined, no indication of any ocelli has been observed.

Antennaria.-- In generalized insects there is a ring-like sclerite surrounding the periphery of each antscoria. In Coleoptera this sclerite is present, but it is distinguished from the head-capsule by a ridge only. On most heads it is considerably reduced in size, about all that can be seen of it externally being its projection, the antscoria, upon which the scape of the antenna articulates. On the other hand, in *Sandalus* (Fig. 167), *Derobrachis* (Fig. 213), *Tetraopes* (Fig. 225), *Leptinotarsa* (Fig. 231) and *Anoplitis* (Fig. 234), the antennaria is quite prominent. The most generalized position of the antennaria is considered to be on the gena cephalad of the eyes, notwithstanding that in generalized insects the antennaria is quite frequently found distinctly between the eyes. Embryology, however, shows that the antennae are postoral in origin. Furthermore, in coleopterous larvae each antennaria is located cephalad of a compound eye. Such a position in coleopterous adults should denote the more generalized condition. The antennaria is very unstable in position. There is hardly a superfamily

in which it does not appear in both the generalized position and elsewhere. In the Scarabaeoidea and Cerambycoidea, though the position of the antennaria varies within certain limits, yet it shows a characteristic location. In the former it is either on the lateral or ventral aspects, while in the latter it occurs only on the dorsal aspect. In no other large groups does the antennaria appear so constant in position. In Calopteron (Fig. 27) and Phengodes (Fig. 29) it is exceptionally large; in Dineutes (Fig. 135) and Alobates (Fig. 202) it is exceptionally small.

Antacoria.-- The membrane attaching the antenna to the head-capsule is the antacoria. In removing the antennae the antacoria is often torn, and as it plays no significant part in this study no attempt was made to represent it in every case. The antacoria varies in size depending upon the size and shape of the scape. It is indicated in a number of figures by the stippled area: Omophron (Fig. 121), Necrophorus (Fig. 134), Calopteron (Fig. 149), Phengodes (Fig. 150), and Chanliognathus (Fig. 146).

Antacava.-- The depression in the vertex, usually in the gena, within which the antennaria and antacoria are situated is the antacava. It is always present, so far as is known, and is developed into a deep socket in Dineutes (Fig. 135), Connophron (Fig. 136), Scolytus (Fig. 245), and Dendroctonus (Fig. 246).

Pretentorina.-- The points of invagination of the pretentoria on the head-capsule are the pretentorinae. They are always located along the epicranial suture in the Coleoptera. In generalized insects and the more generalized Coleoptera, they are situated on the lateral margin of the head. They are therefore represented in this position on the hypothetical type. The pretentorinae have been

identified in every species studied except possibly Calopteron (Fig. 27) and Photinus (Fig. 28). In the latter they are represented by depressions caudad of the eyes. Their position along the epicranial suture varies greatly. In widely separated groups they may be primitively located, as illustrated in such diverse forms as Omophron (Fig. 5), Necrophorus (Fig. 13), Scaphidium (Fig. 23), Chaudoanatus (Fig. 30), Cephaloon (Fig. 37), Macerda (Fig. 25), Ailus (Fig. 44), Phryconomus (Fig. 63), and Glycobius (Fig. 101). The position of the pretentorina evidently cannot possess any important significance in every instance, yet its position may be characteristic sometimes. In the Scarabaeoidea it is never on the dorsal surface; in the Cerambycoidea it is always on the dorsal surface. In this respect, the pretentorinae and the antennariae behave similarly. As a matter of fact they are usually associated together, but there are some striking exceptions. The antennariae of Macrosisgon (Fig. 26) are located well caudad of the cephalic margin of the eyes, while the pretentorinae are situated at the ventro-lateral margin of the head (Fig. 159). The opposite condition is found in Enenolia (Fig. 184). The antennariae in the vast majority of cases are ^{located} caudad of the pretentorinae.

The pretentorinae are the great landmarks of the head-capsule. On their location the determination of the presence and position of the epicranial suture is often dependent, and, consequently, the homologies of large areas of the head-capsule. A case in point is that of the Rhynchophora, in which the pretentorinae are located near the cephalic end of the snout, on the dorso-lateral margin. The epicranial suture is reduced to the very short cephalic ends of the epicranial arms, and though we cannot, therefore, indicate with precision the cephalic limits of the vertex, its approximate limits can be

judged, which would show the vertex to occupy nearly all the dorsal and lateral aspects of the snout. An exception to the above-mentioned position of the pretentorinae is found in the Scolytidae (Figs. ²⁴⁶245) in which the pretentorinae are located in the antacava.

Front.-- The sclerite embraced by the epicranial arms is the front. In the hypothetical type (Fig. /) its caudal and lateral limits are the epicranial arms. Its cephalic limit is indistinguishable since the front is fused with the postclypens. The approximate line of fusion is indicated by a dotted line. There is no indication in any head of a fronto-clypeal suture. The size of the front depends upon the position and direction of the epicranial arms. In those species possessing the inverted Y type of arms, the front assumes considerable proportions, but where the arms have been forced into a more or less straight line across the head, the invagination associated with the epicranial arms includes practically the entire front. As mentioned previously, the epicranial arms extend in this manner across the head in a wide series of families. The front must hence assume this form. In just as wide a series of families, the epicranial arms are in process of disappearing. In such cases, the caudal limits of the front can only be judged approximately. In great reduction of the arms, as represented by *Phalacrus* (Fig. 321) and *Macrosia-gon* (Fig. 159), the vertex, the front and the postclypeus are indistinguishably fused into one area.

Clypeus.-- In all species the clypeus is divided into two distinct sclerites, the postclypeus and the preclypeus. This condition is not present so far as I know in the more generalized insects such as the Orthoptera and Plecoptera. In some Neuroptera, however, the preclypeus is a large characteristic sclerite, quite similar to what has

been designated as the preclypeus in the Coleoptera. It may possibly represent the extraordinary development and differentiation of the labracoria, but its size, shape and form would militate against such an assumption. It seems much easier to believe that this area is a true sclerite, and in this discussion it will be so considered.

Postclypeus.-- The broad cephalic part of the area between the epicranial arms in the hypothetical type (Fig. /) represents the postclypeus. In generalized Coleoptera it is of considerable size if the dorsal surface has retained a generalized form. The shape, form, and size of the postclypeus is correlated with the position and extent of the epicranial arms, which has already been discussed. In highly specialized forms like the Scarabaeoidea (Figs. 9/93), the postclypeus may be even more extensive. Among the Staphylinidae, the postclypeus may be very large in Tachinus (Fig. 17) and Aleochara (Fig. 15), and very small in Creophilus (Fig. 14). In Chalcophora (Fig. 294) the cephalic and of the vertex is located on the ventral aspect of the head, and the postclypeus is reduced to hardly more than a line. Among the Cerambycoidea the postclypeus is generally very large. In Rhynchophora it is quite reduced in size, except possibly in the Scolytidae.

Clypealia.-- The caudo-lateral projection or lobe of the postclypens is the clypealia. In Orthoptera and Plecoptera the clypealia is not separated from the remainder of the postclypens. In the larvae of Corydalis it is a very prominent sclerite. The clypealia in the Coleoptera is often separated from the postclypeus proper by a distinct furrow or suture. It is quite loosely attached to the postclypeus in the Cicindelidae (Figs. 124/125), the Carabidae (Figs. 126/129), many of the Cerambycoidea (Figs. 100/101, 108), and others. Difficulty is often experienced in removing the mandibles from the head without

detaching the clypealia. The close resemblance between the Neuroptera and the Coleoptera in other respects would lead one to believe that this similar structure in the two orders must be homologous. The presence of this furrow in the Coleoptera is wide-spread, as a glance at the figures will show. It can probably show little significance as an indication of primitiveness. It must, though, have been present in the primitive Coleoptera, and is hence shown in the hypothetical type.

Mandibularia.-- In most of the Orthoptera a small triangular area is present, extending from the precoila to the cephalic end of the occipital suture. This sclerite is known as the mandibularia. No such area has been located in the Coleoptera.

Preclypeus.-- The dorsal surface of the larvae of *Corydalis* is very generalized. On this surface there is a prominent submembranous sclerite between the postclypeus and the labrum, the preclypeus. Such a sclerite, very similar in size, form, texture, and position, is present in *Tachinus* (Fig. 17), *Arthromacra* (Fig. 77), *Trichodes* (Fig. 32), and *Glycobius* (Fig. 101). This sclerite is considered the preclypeus. Figure 94 is a longitudinal section of the dorsal aspect of the head of *Harpalus*, and shows the characteristic position of the preclypeus. It is always present in the Coleoptera, though often considerably reduced in size. The preclypeus is always membranous except in *Photinus* (Fig. 28), where it is chitinized and the labrum is membranous. Besides the forms mentioned above, the preclypeus is large and prominent in *Necrophorus* (Fig. 13), *Connophron* (Fig. 16), *Macratria* (Fig. 41), *Philothermus* (Fig. 70), *Hippodamia* (Fig. 76), and many others. Very frequently the cephalic end of the postclypeus is invaginated, thus carrying the preclypeus and the labrum with it. In such cases the preclypeus cannot be seen from the dorsal aspect. The preclypeus, no matter how

deeply it is infolded, is except in a few cases, sharply differentiated from the postclypeus and the labrum. In *Glischrochilus* (Fig. 185) and *Chauliognathus* (Fig. 146) the postclypeus and the labrum were in such close approximation that the preclypeus could not be observed until the two above-mentioned sclerites were separated, and this was possible only after long soaking in potassium hydroxide. In most of the Rhynchophora, due to the fusion or absence of the labrum, the preclypeus could not be identified. The preclypeus, however, was prominent in *Attelabus* (Fig. 120) and somewhat reduced in *Thecesternus* (Fig. 363) and *Epicaerus* (Fig. 364).

Labrum.-- The broad prominent sclerite attached to the cephalic end of the clypeus in generalized insects is the labrum. In Coleoptera possessing other generalized structures, the labrum is typically of the same general form. The labrum is so shown in the hypothetical type. In position the hypothetical labrum should be, with the preclypeus, in accordance with their condition in generalized insects, on the same general level with the remainder of the dorsal surface. The generalized form and position of the labrum is present in every superfamily except the Elateroidea, Dryopoidea, Mysoidea, Scarabaeoidea, and the Rhynchophora in which the postclypeus has been infolded, thus forcing the labrum onto the ventral aspect. All the superfamilies containing species with the labrum generalized, contain about as many with it in various degrees of specialization, as to form, size, texture and position. The labrum in *Connophron* (Fig. 16), *Photinus* (Fig. 28), *Philothermus* (Fig. 70), *Melanophthalmus* (Fig. 74), *Eurygaster* (Fig. 115), and others, are large and membranous. The labrum of *Aphodius* (Fig. 337) is large but very thin and delicate. The labrum of *Scolytus* (Fig. 365) and *Dendroctonus* (Fig. 369) are probably membranous. In the

latter, a significant-looking slightly chitinized structure is located in the membrane within the mouth that may represent the labrum. In *Thecesternus* (Fig. 367) there is a membranous area closely joined to the postclypeus that probably represents the labrum. In *Eupsalis* (Fig. 360), *Lixus* (Fig. 366), *Sphenophorus* (Fig. 368), and *Rhynchites* (Fig. 362), there is an area within the mouth, bounded by furrows, that may be the labrum. Such are particularly suggestive in view of the fact that in the same location and lying flat against the postclypeus a very thin but a relatively large and well chitinized labrum was found in *Epicaerus* (Fig. 364) and *Attelabus* (Fig. 363). The labrum in *Therops* (Fig. 292), *Nosodendron* (Fig. 304), *Phyconomus* (Fig. 309), and *Derobrachus* (Fig. 346) is considerably reduced in size. It is present in every species, except possibly the rhynchophorous genera named above, where it is always said to be wanting.

Occipital foramen.--The prominent opening in the caudal part of the head is known as the occipital foramen. It is generally very large, but in some of the Mordelloidea (Figs. 156/58) and in *Connophron* (Fig. 136), *Cupes* (Fig. 155), and *Rhysodes* (Fig. 182), is reduced in dimensions, due to the constriction of the caudal end of the head. In *Callopteron* (Fig. 149), *Photinus* (Fig. 148), *Alaus* (Fig. 169), and *Tetraopes* (Fig. 225), the occipital foramen is extraordinarily large.

Submentum.--In order to understand clearly the developmental processes that take place on the ventral surface, it is necessary to consider a sclerite, belonging to the mouth-parts, the submentum. In generalized insects the submentum is not only adjacent to but is one of the covering parts of the occipital foramen. Such a position is not found in the Coleoptera. Here, it is always located cephalad of the occipital foramen with a distinct area between the two. In the

vast majority of heads this area is very wide. It is considered as having been present in primitive forms, and is so shown on the hypothetical type. The submentum in generalized insects is a large quadrangular movable plate. Many genera of Coleoptera show a similar size, form, and mobility, as in *Leptinus* (Fig. 258), *Necrophorus* (Fig. 259), the *Staphylinoidae* (Figs. 263, 265), *Necorda* (Fig. 281), *Lyroceroa* (Fig. 287), *Alaus* (Fig. 291), the *Dryopoidae* (Figs. 295, 298), the *Dascilloidea* (Fig. 300), and *Byrrhus* (Fig. 303). In these three characters, and the additional one of position in respect to the paracolla, which in generalized insects is normally found beneath the submentum, that of the *Adephaga* seems to be the most primitive. The innumerable sizes and forms assumed by this structure throughout the entire series of families can best be judged by glancing at the figures. It is extraordinarily large in *Rhysodes* (Fig. 305).

Metatentorina.-- The invaginations on the external surface of the head-capsule of the metatentoria are the metatentorinae. In the *Orthoptera* the metatentorinae are located along the cephalo-lateral border of the occipital foramen as invaginations between the maxillariae and the postgenae. They are not in any way associated with the submentum in generalized insects or in the *Coleoptera*. The same relative position of the metatentorinae is maintained in the *Plecoptera*. In a number of *Coleoptera*, as in *Helichus* (Fig. 296), *Stenelmis* (Fig. 297), *Heterocerus* (Fig. 298), and even in the platystomid, *Eurymycter* (Fig. 361), this same generalized position of the metatentorinae is found. In a number of *Coleoptera* the metatentorinae are situated considerably cephalad of the occipital foramen. The question might be raised as to whether the metatentorinae that are so located could possibly be more generalized in position than those situated adjacent to the

occipital foramen. In every instance in which the metatentorinae are located cephalad of the occipital foramen, a suture connects the metatentorinae with the foramen. In only a few cases does the suture extend much farther cephalad than the metatentorinae. This suture in the vast majority of heads studied does not extend cephalad. It is readily seen how the metatentorinae might be drawn cephalad and as a result a suture be formed marking their line of migration. In such a process one would naturally not expect to find a suture located cephalad of the metatentorinae, and in the cases in which the suture does extend so it is easy to understand that the force of the cephalic pull might have been communicated to this region, producing in consequence a suture or invagination. Due to the shape of the head, it is most difficult to believe that the metatentorinae could be drawn caudad, and if they were so drawn, it would seem that in this process there would be formed a suture cephalad of the metatentorinae, marking the line of migration. In this discussion the generalized position of the metatentorinae will be considered as that of their generalized position in more primitive insects, at or near the occipital foramen.

In the development of the coleopterous head the metatentorinae have shown a tendency to migrate cephalad. The cephalic migration of the metatentorinae and the ventral migration of the pretentorinae and other structures, were no doubt due to the same force, the result being a closer approximation of parts, which naturally supplied increased firmness to the head's mechanics of operation. The Dryopoidea show the most generalized position of the metatentorinae. Genera of this superfamily have been mentioned above. The Elateroidea probably possess the next most generalized metatentorinae, such as in

Sandalus (Fig.289) and Alsus (Fig.291). The Cucujoidea show the metatentorinae just a little removed from the occipital foramen, as in Megalodacne (Fig.312), Anchicera (Fig.314), Philothermus (Fig.317), and others. In the genera of other superfamilies, as Nosodendron (Fig.309), Anoplitis (Fig.357), and Tetraopes (Fig.348), almost the same degree of primitiveness is shown. The large superfamily Mordelloidea show the metatentorinae to have migrated to about half the distance between the occipital foramen and the submentum. This condition is fairly consistent through the group. In the Bostrichoides, the Scarabaeoidea, and the Cerambycoidea, the metatentorinae show considerable variation in position. This is shown by a comparison of their position in Bostrichus (Fig.333) and Spindus (Fig.335). In the families to which Tetracha (Fig.248), Calosoma (Fig.250), Cybister (Fig.254), Dineutes (Fig.255), Necrophorus (Fig.259), and Glicobius (Fig.347) belong, the metatentorinae have advanced very far cephalad, near to the submentum. In Photinus (Fig.272) and Chauliornathus (Fig.274) they are located on or quite near the paracosta.

Maxillaria.-- There is a narrow plate surrounding the lateral and caudal margins of the occipital foramen in some generalized insects, between which and the postgenae the metatentorinae are invaginated. This plate has disappeared in the Coleoptera.

Cervix.-- The structure connecting the head-capsule with the prothorax is called the cervix. It is normally composed of membrane, and a number of cervical sclerites. The size of the cervix depends upon the size of the occipital foramen, and the degree of mobility of the head. In the Lampyroidea and some other forms the cervix is very large. The cervix in Rhysodes (Fig.305) is composed of tough fibrous membrane, quite different in structure from the normal cervix. In

nearly all of the Rhynchophora the cervix is heavily supported by strong tendons attached at its cephalic end. These tendons take care of the added strain on the cervix due to the elongation of the snout. There are more or less small cervical tendons appearing occasionally throughout the whole series of families studied. In *Molamba* (Fig. 261) the cervix is invaginated within the prothorax, doubling upon itself. The cervix in *Bostrichus* (Fig. 333) doubles back upon the head-capsule, which is produced into a round projection.

Cervical sclerites.-- The most prominent and persistent cervical sclerites are the pleural cervical sclerites, the cervicisternum and the cervicimeron. The former is usually the larger of the two, and articulates at its cephalic end either against an odontoides or simply against the undifferentiated area surrounded by the occipital foramen. The latter usually extends in a different direction from the former, and articulates at its cephalic end with the cervicisternum and at its caudal end with the prothorax. In *Cantharis* (Fig. 275), *Macratia* (Fig. 288), *Psephenus* (Fig. 295), and others there is a single large sclerite present. In the Adephaga, in *Leptinus* (Fig. 258), *Hyporhagus* (Fig. 329), *Phyconurus* (Fig. 309), *Pseudocistela* (Fig. 324), and many others, there is a single small subcircular sclerite present. Both of these types probably represent the cervicisternum. In a very large number of genera cervical sclerites are always wanting. They are poorly or not at all developed in the Cerambycoidea. None of the Rhynchophora studied possess a cervical sclerite except *Eurymycter* (Fig. 361), in which it is very small. The ventral cervical sclerite is the cervicisternum. *Nacorda* (Fig. 281), *Cucujus* (Fig. 310), *Hister* (Fig. 270), *Tenebrio* (Fig. 326) and a few others, possess two small small cervicisterna, while *Tomoxia* (Fig. 282) possesses a long narrow one. The

cervisternum is on the whole of infrequent occurrence. The dorsal cervical sclerite is called the cervinotum. It occurs even less frequently than the cervisternum. Hydrous (Fig. 11) possesses a subquadrangular distinctly chitinized cervinotum. In Aleochara (Fig. 15) the cervinotum is divided into two distinct lightly chitinized subtriangular sclerites. Two much larger square-like sclerites are situated caudad of these. All of the Hydrophilidae and Scarabaeidae possess setaceous caudo-lateral sclerites, which do not seem to be present in other genera studied.

Odontoidea.-- Owing to the strong chitinization of the head and the close fit of the head in the prothorax, there is little need for a special process or projection on the head for the articulation of the cervisternum. Such a process is called an odontoidea. The few instances in which it does occur are in Scaphidium (Fig. 37), Eubinetus (Fig. 42), Cyphon (Fig. 422), Byrrhus (Fig. 424), Nosodendron (Fig. 425), Phyconomus (Fig. 430) and Arthromacra (Fig. 449). The latter genus, it is interesting to note, possesses no cervisternum.

Postgena.-- That part of the head-capsule on the caudal surface, mesad of the occipital suture and ventrad of the occiput, in generalized orthopterous insects is the postgena. The occiput is considered as extending to near the middle of the dorso-ventral length of the occipital foramen, thus limiting the dorsal extent of the postgenae. The latter are widely separated from each other by the occipital foramen. The lateral parts of the large submentum distinctly cover the mesal parts of the postgenae. In the Coleoptera the occipital suture separates this region from the remainder of the head-capsule, as in generalized insects, and the occiput is also indistinguishably fused with the postgenae. But the postgenae, instead of being widely sep-

arated and their mesal parts being covered by the lateral parts of the submentum are directly connected by the broad area located between the occipital foramen and the submentum (Fig. /); and the submentum is attached to the mesal portion of the cephalic margin of the postgenae. This area is indistinguishably fused with and undifferentiated from the postgenae in the hypothetical and the more generalized types of ventral surface.

In generalized insects the submentum is joined to the cervix by the undifferentiated part of the cervix, the cervicoria. In the cephalic migration of the submentum, a part or all of the cervicoria must have been drawn in behind. The postgenae alone bordered the lateral margins of the submentum and the cervicoria. A possible line of development may have been the chitinization of the cervicoria and the disappearance of the sutures separating it from the postgenae. The broad area between the occipital foramen and the submentum would in such a case be a modification of part or all of the cervicoria. It is much easier to believe, instead, that because of the membranous condition of the cervicoria, no strong resistance was offered to an approach of the mesal margins of the chitinous postgenae, which would migrate thus to serve as a firm foundational support for the submentum, as well as to strengthen the solidity of the head-capsule as a whole. The mesal margins would in time approach so close as to press the two sides of the cervicoria into a line. Fusion of the mesal margins of the postgenae would finally take place, and the cervicoria would be divided into two parts. One part would be attached to the submentum entirely separated from that portion of the cervicoria bordering the occipital foramen, and would be finally reduced to a suture. The other part of the cervicoria would remain as a portion of

the cervix. Whether the mesal margins of the postgenae would approach the meson as broad surfaces, or as narrow ones and later elongate, it would be difficult to state with certainty, though the latter would probably happen. In the primitive coleopterous head it is not unlikely that the head was much shorter, and that the area between the occipital foramen and the submentum was correspondingly shorter, so that there would not be the necessity for a broad fusion of the mesal margin of the postgenae. So far as observed there has been retained in no coleopterous head any marks of the line of fusion of the postgenae.

Abundant evidence is found for the conclusion that the broad area between the occipital foramen and the submentum must be a part of the postgenae. A similar condition as in the Coleoptera is present in many families of insects. In many Hymenoptera the mesal margins of the postgenae are fused between the occipital foramen and the articulation of the labium. That this is the true interpretation of this structure is shown by the fact that there is often a suture on the meson showing the line of fusion, and is further substantiated by the fact that this area bears on its ventral margin the paracollae. In all cyclorrhaphous and orthorrhaphous Diptera the area ventrad of the occipital foramen is a continuous chitinized piece, similar to that found in the Coleoptera, and is derived from the fusion of the mesal margins of the postgenae.

It may be well to add here that the expression "cephalic migration" as applied to the changed location of such a structure as the submentum, may be only relatively correct in its suggestion. Very probably the occipital foramen in Coleoptera has migrated dorsad, at least it has assumed this typical position. Such a migration in

itself would produce an elongation of the ventral surface, with a consequent production of the broad area between the occipital foramen and the submentum. Whether the force exerted on the head was directed more towards the cephalization of the submentum or towards the dorsalization of the occipital foramen it would be hard to say. The condition resulting would be in either case approximately the same. For purposes of convenience and simplicity of language, the expression "cephalic migration" is used in this discussion.

This broad area between the occipital foramen and the submentum is sometimes designated as the gula. Usually, though, the term gula is used to indicate a sclerite, on the meson of the ventral aspect, separated from the remainder of the head-capsule by distinct subparallel sutures, the gular sutures. The term gula cannot satisfactorily be applied to both an indefinite region and a distinct sclerite. The gula is considered in the latter sense in this discussion. For the present the area between the occipital foramen and the submentum will simply be designated as the mesal parts of the postgenae.

The cephalic end of a postgena is usually modified into a rather flat area sloping towards the meson, upon which are situated a paracolla and a postcolla. This flat area is distinguished from the remainder of the postgena by a distinct ridge, which usually extends in a deep curve from near the lateral margin of a postcolla to near the caudo-lateral margin of the submentum. Sometimes this ridge is directed towards the occipital foramen, as in *Leptinus* (Fig. 258), *Cantharis* (Fig. 275), *Macrosiagon* (Fig. 283), *Therops* (Fig. 292), *Psephenus* (Fig. 295), *Helichus* (Fig. 296), and others. Attention has already been called to the fact that the cephalic portion of this ridge represents the cephalic end of the occipital suture. This modified part is

reduced in size or indistinguishably fused with the remainder of the head, in *Photinus* (Fig. 272), *Eucinetus* (Fig. 300), *Alobates* (Fig. 325), *Tenebrio* (Fig. 326), *Hyporhagus* (Fig. 329), most of the *Leucobaeoidea*, *Sphenophorus* (Fig. 368), *Eupsalis* (Fig. 360), and *Ilixus* (Fig. 366).

Gula.-- There seems to be considerable confusion as to what constitutes the gula. Some investigators consider it as simply the central portion of the ventral surface of the head-capsule. Others restrict it to the distinct sclerite appearing on the meson of the ventral surface of certain insects, including the Coleoptera. Since this sclerite is distinctive and characteristic it needs a name. The term gula is quite satisfactory to apply to it. The origin of the gula also rests in considerable confusion. Comstock and Zochi (1902) consider it the sternum of the cervical segment, and to strengthen their argument they cite the situation in *Corydalis*, in which they state that the sternellum of the cervical segment is retained back of the gula, and they figure it as the small quadrangular sclerite immediately caudad of the gula. They do not mention the very much larger rectangular cervical sclerite caudad of their "sternellum". The larger sclerite is suggestive of the sternellum, and the smaller one would then represent their "sternum". It is generally stated that the gula is derived from ^{the} chitinization of the neck membrane or cervix. In the discussion preceding, dealing with the metatentorinae and the postgenae, I have attempted to show the impossibility of such a derivation. In many orders of insects structures on the caudal aspect of the head have been designated as the gula. My interpretation would prevent the recognition of the presence of the gula in any insects other than the Coleoptera, Neuroptera, Trichoptera, and possibly the Mecoptera.

practically

In some Coleoptera there is ^{practically} no gula (Figs. 267, 297), whereas in others there is a complete gula (Figs. 251, 256). Between these extreme types there are found in the Coleoptera all gradations of a gula in process of formation (Figs. 291, 286, 333). Such a range of variation in a structure simply emphasizes the importance of a comparative study of a large series of forms. The question as to which is the more generalized condition, the presence of a complete gula or the absence of one, has been discussed previously, with the verdict in favor of the latter condition. It would then be impossible, other reasons not being considered, for the gula to be the sternum of the cervical segment. The gula is the sclerite formed by the migration of the metatentorinae from the occipital foramen towards the submentum, and must be derived from the postgenae. In this migration of the metatentorinae sutures are produced which are known as the gular sutures. The area between the gular sutures is the gula. It is evident, then, that the presence and extent of the gula depend upon the position of the metatentorinae and the sutures which they produce. The gula is complete in all the Adephaga except Peltodytes (Fig. 253), in the Silphidae, the Staphylinidae, the Sphaeriidae, the first four families of the Cantharoidea, and the Scarabaeidae, except Pseudolucanus (Fig. 343). Isolated examples in other families of a complete gula are Scaphidium (Fig. 269), Helichus (Fig. 296), Cyphon (Fig. 301), Byrrhus (Fig. 303), and Leptinotarsa (Fig. 354). The gular sutures nearly meet in Gasterolobium (Fig. 263) and Creophilus (Fig. 264), and are entirely confluent in Necrophorus (Fig. 259), Scaphidium (Fig. 269), Hister (Fig. 270), Phengodes (Fig. 273), Chauiognathus (Fig. 274), and in all the Rhyngophora except Eurymycter (Fig. 361), in which genus the gular sutures are very short and widely separated. The gula in cases of con-

fluency of the middle portion of the gular sutures on the meson is simply invaginated. The gula is complete but extremely short in Calopteron (Fig. 271) and Photinus (Fig. 272). The cephalic ends of the gular sutures meet on the meson near the occipital foramen in Philothermus (Fig. 317) and Anoplitis (Fig. 357). The gula is partially membranous in Mesodendron (Fig. 304), Litodrepa (Fig. 332) and Hesiocis (Fig. 336). Part of it is deeply invaginated transversely in Scaphidium (Fig. 269), Chauliognathus (Fig. 151), Helichus (Fig. 296), Stenelmis (Fig. 297), and others.

Epicranium.-- Most of the sclerites of the head-capsule are so closely united in some Coleoptera as to appear as a single piece. Straus-Durckheim (1888) so regarded this region in the head-capsule of the May-beetle, and named it the epicranium. Used in the sense of indicating a closely united area, the term seems satisfactory and may often prove convenient. It can then be only a relative term, including at times no more than the paired sclerites of the head, when the epicranial suture is well developed. Occasionally, the preclypeus and the labrum are closely joined to the head-capsule. In such cases the epicranium would embrace these structures, also.

Paracoila.-- The small rather concave projections at the caudomesal margins of the postgenae against which the maxillae articulate are the paracoilae. They are usually easily identified, as in Molam-ba (Fig. 261), Pytho (Fig. 286), Heterocerus (Fig. 298), and Rhymaphora (Fig. 319). They are usually chitinized, but are membranous in a considerable number of genera. The paracoilae are insignificant in size in Gastrolobium (Fig. 263), all of the Elateroidea, Listela (Fig. 324), and Tenebrio (Fig. 326). In generalized insects the paracoilae are situated beneath the submentum. They are found in a similar position in

the Adephaga (Figs. 249, 251), in Hydrous (Fig. 256), and a few others. They are also always located on the postgenae in generalized insects. This position is of great importance in determining the identity of the postgenae in specialized insects.

Postcoila.-- At the cephalic end of a postgena is always found a distinct crescent-shaped acetabulum-- the postcoila, against which the postartis of the mandible articulates. Throughout the genera the postcoilae exhibit some degree of difference in exact position upon the postgenae, in size, and in degree of shallowness. Their form and position are indicated in Calosoma (Fig. 250), Sphaerius (Fig. 268), Moxotus (Fig. 290), and Derobrachus (Fig. 346). In generalized insects the postcoila are also always located on the postgenae, and their position is of equal importance with that of the precoilae in determining the identity of the postgenae.

Precoila.-- The rounded condyle on the ventral surface of each clypealia, against which the preartis of the mandible articulates is the precoila. It is usually crescent-shaped, but sometimes, as in Peltodytes (Fig. 253), Cybister (Fig. 254), Creophilus (Fig. 269), Endomychus (Fig. 320), Dichelonyx (Fig. 338), and others, the form is spherical. The precoilae are large in Macrasiagon (Fig. 283), Epicauta (Fig. 284), Tharops (Fig. 292), Chaulioognathus (Fig. 274), Bostrichus (Fig. 333), and others, and small in Dineutes (Fig. 255), Photinus (Fig. 272), Helichus (Fig. 296), Derodontus (Fig. 313), and particularly so in Isephenus (Fig. 295). The precoilae can readily be recognized by their characteristic form. Since they are always located on the caudo-lateral lobe of the postclypeus, or the clypealia of certain insects, they are a great aid in determining the limits of the postclypeus.

Tentorium.-- The endoskeleton of the head is known as the ten-

torium. It is composed of two anterior and two posterior arms or projections, and their various modifications. The anterior arms arise from the pretentorinae, and are known as the pretentoria. The posterior arms arise from the metatentorinae, and are known as the metatentoria. In generalized insects one end of the pretentoria expand along and are continuous with the epicranial suture. Each extends in a caudo-mesal direction, and narrows for a short distance, then expands along its mesal margin until a fusion is formed with the pretentorium of the other side, producing the cephalic bridge or laminatentorium. The pretentoria separate and then fuse again farther caudad with each metatentorium. The metatentoria extend cephalo-mesad a very short distance, their mesal margins expand and completely fuse on the meson, producing the caudal bridge, or corpotentorium. The fusion of the pretentoria and the metatentoria is supposed to take place along the cephalic margin of the corpotentorium. The dorsal projections arising from the lateral margins of the pretentoria and extending toward and attached to the dorsal wall of the head, are the supertentoria. The ring-like plate surrounding the inside periphery of the occipital foramen is indistinguishably fused with and is a part of the metatentoria. The tentoria, as a whole, are distinctly chitinized and well-developed. The typical condition of the tentorium in generalized insects is practically duplicated among the Coleoptera. The hypothetical type (Fig. 370) has been constructed with this similarity in mind. The greatest difficulty experienced was in deciding upon the primitive type of laminatentorium, whether it should be represented as complete or incomplete, that is, whether the two sides of the laminatentorium fuse on the meson or not. Many Coleoptera that in other respects are quite generalized do not show a com-

plete laminatentorium, as *Tetracha* (Fig. 371), *Onophron* (Fig. 375), *Di-neutes* (Fig. 378), *Leptinus* (Fig. 381), *Tachinus* (Fig. 387), and *Stenelmis* (Fig. 418). The hypothetical laminatentorium is represented as nearly meeting on the meson. At least, such a condition is thought to be not far removed from that which actually existed in the primitive Coleoptera. *Limulodes* (Fig. 389), *Eurystethis* (Fig. 406), *Pytho* (Fig. 407), *Philothermus* (Fig. 438), *Melanophthelma* (Fig. 439), *Hyporhagus* (Fig. 450), *Sphindus* (Fig. 456), and others, possess practically no trace of a laminatentorium, but well-developed supratentoria. The latter are fairly well developed in *Photinus* (Fig. 399), *Collops* (Fig. 397), and *Alaus* (Fig. 412), but there is neither a laminatentorium nor a corpotentorium present. There is no trace of any one of the three above-mentioned structures in *Tharops* (Fig. 413) and *Throscus* (Fig. 414). *Phalacrus* (Fig. 442) and *Eurymycter* (Fig. 483) possess only the rudiments of the pretentoria and metatentoria. The tentoria of the *Cerambycoidea* (Figs. 471, 479) are very delicate and membranous. The pretentoria, the metatentoria, and the corpotentoria are always complete, while the laminatentorium and supratentoria are always either rudimentary or absent except in *Eachymerus* (Fig. 480), in which the supratentoria are present. Other genera showing completely membranous tentoria are numerous. Among these are *Cupes* (Fig. 400), *Eurystethus* (Fig. 406), *Rhodes* (Fig. 426), *Languria* (Fig. 432), and *Pseudocistela* (Fig. 445).

Pretentorium.-- A generalized condition of the pretentorium, characterized by a strong chitinization as a whole, and possessing a broad flaring cephalic end, is found in the *Adephaga* (Figs. 374, 377), *Leptinus* (Fig. 381), *Necrophorus* (Fig. 382), the *Staphylinidae* (Figs. 385, 386), *Georysus* (Fig. 420), *Eucinetus* (Fig. 421), *Dermestes* (Fig. 423), and *Derodontus* (Fig. 434). There are all degrees of gradation present

from the most generalized pretentoria to those very delicate membranous ones represented by such forms as *Heterocerus* (Fig. 419), *Endomychus* (Fig. 441), *Pseudocistela* (Fig. 445), *Hyporhagus* (Fig. 450), the majority of the *Cerambycoidea*, and the *Rhynchophora*. A very prevalent type, possessing a distinctly chitinized cephalic end and a membranous caudal portion sharply separated from the former, is represented in *Epicauta* (Fig. 405), *Pytho* (Fig. 407), *Chalcophora* (Fig. 415), *Alobates* (Fig. 446), *Bostrichus* (Fig. 454), *Diabrotica* (Fig. 478), *Dendroctonus* (Fig. 491), and most of the *Scarabaeoidea*. Rudimentary pretentoria are found in a number of genera, as *Calopteron* (Fig. 393), *Tenebroides* (Fig. 427), *Phalacrus* (Fig. 442), and perhaps all of the *Rhynchophora*, except *Dendroctonus*. The pretentoria of the *Rhynchophora* are for the most part very delicate and fragile. The difficulty of making a dissection showing the pretentoria intact is intensified by the close packing withⁱⁿ the snout of the greatly developed tendons of the mouth parts and the strongly chitinized pharynx. In no instance, except in *Dendroctonus* (Fig. 491) was a pretentorium preserved intact. In *Scolytus* (Fig. 490) the pretentorium is evidently rudimentary, but in none of the other genera is there a clear indication of such being the case, owing to the presence of frayed ends, suggesting that not all of the pretentorium has been seen. The presence in the *Rhynchophora* (Figs. 488, 489) of a suture in the right position for an epicranial suture, an invagination within the suture that suggests the pretentorium, and a projection arising from the invagination, all furnish evidence that this projection is probably the cephalic portion of the pretentorium. The pretentorium of *Passalus* is extraordinarily developed. The cephalic part extends as a slender bar dorso-caudad, nearly half way to the occipital foramen, then bends sudden-

ly and extends as a huge straight arm toward the corpotentorium. The tremendous development of the caudal part is due to the need of a strong support for the dorsal surface, which bears a prominent horn used in fighting.

Metatentorium.-- The form and size of the metatentorium is quite decidedly indicated by the position of the metatentorinae. Those genera possessing primitive metatentorinae are very apt to possess the primitive type of metatentorium, one that is short and simple, as *Limulodes* (Fig. 389), *Sphaerius* (Fig. 390), *Anchicera* (Fig. 435), *Philotermus* (Fig. 438), *Melanophthalma* (Fig. 439), and *Sphindus* (Fig. 452). It is significant to note that all of these genera are very small in size. The cephalic migration of the metatentorinae is due to a similar movement of the metatentoria. In those genera in which the metatentorinae have migrated from their primitive position near the occipital foramen, the metatentoria are found more or less deeply invaginated along the gular sutures, the sutures being the products of these invaginations. In most genera the metatentoria advance but little or not at all farther cephalad than the metatentorinae, but there are some exceptions, in which the metatentoria taper down gradually, as in *Helichus* (Fig. 417), *Cyphon* (Fig. 422), *Lyctus* (Fig. 455), and all of the *Scarabaeoidea*, except *Pseudolucanus* (Fig. 469). In those genera in which the gular sutures are confluent on the meson, the gula itself is simply invaginated, becoming a part of the metatentorium. The same type of development has taken place in *Necrophorus* (Fig. 382), *Scaphidium* (Fig. 391), *Hister* (Fig. 392), *Pnengodes* (Fig. 395), *Chauliognathus* (Fig. 396), and *Georyssus* (Fig. 420), as in the *Rhyncho-phora*. In *Necrophorus*, *Pnengodes*, *Chauliognathus*, *Lupsalis* (Fig. 482), and *Thecestermus* (Fig. 487), the line of fusion of the invaginations

of the two sides has disappeared. In *Chauliognathus* the invagination is greatly reduced, and in *Rhengodes* nothing remains but a mere line. These two latter genera seem to show a greater specialization of the gular region than any other genera studied. A correspondingly deeper invagination of the ring-like plate surrounding the inside periphery of the occipital foramen has occurred with that of the gula. The whole phenomenon appears to be due to an especially strong cephalic pull on the metatentoria. This can be readily understood in the case of the *Rhynchophora*, in which the elongation of the snout would encourage this result. A second force may play a part here, that of the narrowing of the snout, which might assist in the enfoldment of the gula.

A large number of genera, scattered throughout the series of families, possess prominent projections along the mesal margins of the metatentoria, caudad of the corpotentorium, as those of *Cybister* (Fig. 377), *Necrobis* (Fig. 399), *Glischrochilus* (Fig. 429), *Rhyconomus* (Fig. 430), and *Boros* (Fig. 448). Some of these projections have distinct tendons attached to them, as in *Scaphidium* (Fig. 391), *Parandra* (Fig. 467), *Derobrachus* (Fig. 468), *Donacia* (Fig. 477), and *Crioceris* (Fig. 473). Prominent lateral projections are present in *Lyctus* (Fig. 453), *Osmoderma* (Fig. 462), *Parandra*, *Glycobius* (Fig. 469), *Rhynchites* (Fig. 484), *Epicaerus* (Fig. 486), and *Thecesternus* (Fig. 487). *Passalus* (Fig. 466) is peculiar in the possession of a large well-chitinized secondary bridge arising from the mesal margin of the metatentoria.

Corpotentorium.-- Owing to the simplicity of form of a structure like the corpotentorium, but little change is indicated in it through most of the genera. The hypothetical type shows this structure to be a rather narrow simple band (Fig. 370). Such is fairly

characteristic of the vast majority of forms. The corpotentorium is sometimes very broad, as in *Ptinus* (Fig. 452), *Bostrichus* (Fig. 454), *Parandra* (Fig. 467), *Derabrachus* (Fig. 468), *Glycobius* (Fig. 469), and *Eup-salis* (Fig. 482). In contrast are many that are quite slender and arched, as *Dineutes* (Fig. 378), *Stenus* (Fig. 384), *Hister* (Fig. 392), *Geor-ryssus* (Fig. 420), and *Mycetophagus* (Fig. 437). The form of these latter has evidently resulted from the narrowing of the space between the metatentoria. An exceptionally large number of genera have only a rudimentary corpotentorium, or none at all, as in all of the Lampy-roidea except *Trichides* (Fig. 398) and *Necrobia* (Fig. 399), *Epicaute* (Fig. 405), *Macrosiagon* (Fig. 404), all of the Elateroidea, *Psephenus* (Fig. 416), *Rhysodes* (Fig. 426), *Phalacrus* (Fig. 442), *Hippodamia* (Fig. 443), and *Ar-thromacra* (Fig. 449). The reasons for the loss of the corpotentorium are not always evident, though in most cases, either the arms of the tentoria have expanded and approximately met on the meson, as in *Rhy-sodes* and *Plesiocis* (Fig. 457), or the arms are directed towards the meson and meet there, as in *Connophron* (Fig. 383) and all of the Elat-eroidea, or the pharynx rests snugly between the tentorial arms, as is so perfectly found in *Chauliognathus*, where the pharynx is wedged so tightly between them that the whole seem like one piece, all of which conditions supply firmness to the tentorial arms and obviate the necessity for a corpotentorium. Of the Rhynchophora, *Eurygaster* (Fig. 483), *Epicaerus* (Fig. 486), and *Lixus* (Fig. 488) possess no corpoten-torium. *Scolytus* (Fig. 490) possesses a very rudimentary one. The disappearance of the corpotentorium can best be explained in the case of the Rhynchophora by the fusion of the metatentoria into one solid plate that needs no added support. The corpotentorium of most of the Cerambycoidea is a delicate membranous structure. A common modifi-

cation of the cornuotensorium is the mesal projections on its cephalic border, as in *Tachinus* (Fig. 387), *Cephaloon* (Fig. 401), *Tomoxia* (Fig. 403), *Phenolia* (Fig. 428), and *Philothermus* (Fig. 438).

Laminatentorium.-- A structure of the tentorium that shows perhaps a greater variability in form than any other is the laminatentorium, which appears in a great array of shapes and sizes, from the forming of a perfect and broad bridge to total disappearance. When the two sides of the laminatentorium meet on the meson, the mesal margins of the laminatentorium very frequently are bent ventrad, producing a projection. Examples of this development are seen in *Calosoma* (Fig. 373), *Cybister* (Fig. 377), *Necrophorus* (Fig. 382), *Aleochara* (Fig. 388), *Heterocerus* (Fig. 419), *Dermestes* (Fig. 423), and *Endomychus* (Fig. 441). Genera that show the laminatentorium as hardly more than touching on the meson are *Peltothytes* (Fig. 376), *Scaphidium* (Fig. 391), *Pyrochroa* (Fig. 408), *Notoxus* (Fig. 410), *Psephenus* (Fig. 416), *Cucujus* (Fig. 431), *Penthe* (Fig. 457), and most of the *Scarabaeidae*. The reduction of the laminatentorium takes place so gradually that it is hard to tell when it has completely disappeared. There seems to be no indication of it in *Limulodes* (Fig. 389), *Collops* (Fig. 397), *Pseudocistella* (Fig. 445), *Hyporhagus* (Fig. 450), *Sphindus* (Fig. 456), and others. In *Tomoxia* (Fig. 403), *Pytho* (Fig. 407), *Alaus* (Fig. 412), *Tharops* (Fig. 413), *Throscus* (Fig. 414), and others there is no laminatentorium. The pre-tentorial arms curve towards the meson and serve a similar purpose. The laminatentorium of *Tachinus* and *Epiesuta* (Fig. 405) is in the form of a lobe. That of *Psephenus* (Fig. 416), *Dichelonyx* (Fig. 459), and *Pelidnota* (Fig. 460) possesses two long sharp cephalic projections.

Supratentorium.-- Arising from the dorsal surface of each pre-tentorium cephalad of the laminatentorium and usually extending

towards the dorsal surface of the head is a projection of variable form, the supratentorium. Its generalized condition would show a rather distinctly chitinized structure, with an expanded ventral end that gradually narrows, then expands flat-like against the ental surface of the head-wall. This kind of structure is found in a very large number of genera, as all of the Adephaga except Peltodytes (Fig. 376), the Hydrophilidae, Leptinus (Fig. 381), all of the Staphylinoidae except Aleochara (Fig. 388) and Hister (Fig. 392), Pytho (Fig. 407), Nosodendron (Fig. 425), Languria (Fig. 432), Megalodacne (Fig. 433), Derobrachus (Fig. 468), and others. The supratentorium is a surprisingly persistent structure considering the large number of genera that possess it in a more or less rudimentary state. The broken ends of the tentoria of Eupsalis (Fig. 482), Lixus (Fig. 488), and Sphenophorus (Fig. 489) are expanded, which expansion may include a part of the supratentoria. This seems reasonable to believe when a rudimentary one is evidently present in Rhynchites (Fig. 484) and Attelabus (Fig. 485). Sphenophorus is peculiar in having the lateral margins of the tentoria fused to the oculata. The head-capsule of this genus is suddenly constricted at this point, which probably placed the tentorium and head-wall in contact, a fusion finally resulting. The supratentoria of Cucujus (Fig. 431) and Passalus are stout structures, but extremely short. In the former, this condition is due to the flatness of the head, in the latter, to the unusually close proximity of a part of the pretentoria to the dorsal surface.

V. SOME PHYLOGENETIC CONSIDERATIONS

With the hypothetical type of coleopterous head in mind, it is possible to note the lines of development that have taken place within the various groups. Structures have developed away from the prim-

itive condition with varying degrees of rapidity, and sometimes in different directions. It is difficult from this study to decide on the amount of importance to attach to the change that may take place in a particular structure, and to average the degree of primitiveness as a whole of the development of the structures characteristic of a group, and to indicate with precision the place in the primitive scale of each group. As previously mentioned, owing to the wide field covered in this investigation it was impossible to find time to study a large representation of genera within each family. Such a study should help one considerably in reaching clearer conclusions as to the arrangement of the genera in the primitive scale. Using this study as a basis, it is quite possible, however, to discuss the relative importance of the structural changes exhibited by the different groups, and to suggest possible inconsistencies in the present arrangement of certain genera.

Adephaga.--The characteristic possession of the occipital suture, of complete epicranial arms, of a generalized position of the antennariae and of the pretentorinae, of a generalized form of labrum and of tentorium, would force such families as the Cicindelidae, Carabidae, Amphizoidae and Omophronidae into a primitive place in the phylogenetic scale, in spite of their specialized ventral surface. No other large group shows as many primitive characters. The genera of the above-mentioned families show a great similarity in all their structures and must be closely related. Of these families Omophron possibly possesses the most generalized dorsal surface, though the occipital suture in this genus is not nearly complete, and does not show on this surface. Omophron can hardly hold an intermediate position between the Carabidae and the Heliophilidae, for the latter

latter family, as represented by Peltodytes, shows little similarity with any other family of the Adephaga. The form of the head is distinctly specialized, being globular, with enormous eyes, and the mouth-parts and the very small labrum are directed distinctly ventrad. The occipital suture is probably lacking, the epicranial suture is shorter than in any other genus of the Adephaga. On the ventral surface, the metatentorinae extend only halfway between the occipital foramen and the submentum, and the gular sutures extend no farther cephalad, whereas in all the other genera of the Adephaga the metatentorinae are close to the submentum and complete gular sutures are present. Finally, the tentorium of Peltodytes is not so well developed, and the supratentoria are small and do not reach the ventral surface of the head wall. In all other genera of the Adephaga the tentorium is large and strongly chitinized in all its parts. The Dytiscidae and Gyrinidae are very similar fundamentally, and differ from other adephagous families in the position on the ventral aspect of such structures as the antennariae and the pretentorinae, and by a rudimentary or absent occipital suture. The instability of the epicranial suture is well illustrated by the case of the two closely related genera, Dytiscus and Cybister, the former possessing complete, distinct arms, and a considerable part of the caudal end of the stem, the latter incomplete and rather indistinct arms and no part of the stem. The Dytiscidae and the Gyrinidae are undoubtedly more specialized than the first four families of the Adephaga.

Hydrophiloidae.—The form and texture of the head of the Hydrophilidae is quite similar to that of the Dytiscidae and Gyrinidae. The heads of all these families are broad and short and strongly chitinized. The antennariae and pretentorinae of the Hydrophilidae

have migrated ventrad, as in the other two families. The metatentorinae, the gula, and the tentorium are almost identical in form and condition, also. This superfamily is evidently very closely related to the Dytiscidae and Gyrinidae.

Silphoidea.-- The genera of the Silphoidea show many inconsistencies. The dorsal and ventral surfaces and the endoskeleton of no two genera are nearly alike. Necrophorus possesses the most generalized dorsal surface, which is very like that of the first four families of the Adephaga. On the other hand, this genus possesses the most specialized ventral surface present in this superfamily. The gular sutures are complete, and for more than half their extent meet on the meson. In contrast, there are practically no gular sutures in Connophron, a scydmaenid, and Molamba, a corylophid. No greater extremes of this surface can be found within the limits of any other superfamily. The tentorium exhibits just as great extremes in development. That of Leptinus is quite generalized; that of Necrophorus well developed but specialized, owing to the invagination of the gula; that of Connophron with no corpotentorium nor laminotentorium and rudimentary supratentoria; that of Molamba the most rudimentary tentorium of any genus included within this study. No clearer illustration of the difficulties of indicating relationship can be shown than that exhibited by the families of the Silphoidea.

Staphylinoidae.-- The various genera of the Staphylinidae show considerable homogeneity. Tachinus departs the most from the characteristic condition, in possessing a much more generalized dorsal surface than the other members of this family. The Staphylinidae possess a tentorium and a ventral surface similar on the whole to that of the Adephaga and the Hydrophiloidae. Tachinus, through the added

similarity of its dorsal surface, would seem to bear a particularly close relationship to these groups. The Sphaeriidae, as represented by Sphaerius, and the Ptilidae, as represented by Limulodes, possess a primitive condition of the metatentorinae, while Scaphidium and Hister possess confluent gular sutures. The Pselaphidae, as represented by Pilopius, in form of head and character of the ventral surface and tentorium shows a close relationship to Connophron. The irregularities of structure displayed by the families of this group are nearly as great as those displayed by the families of the Silphoidea. Both of these superfamilies probably need considerable revising.

Cantharoidea.-- All of the genera of the Cantharoidea possess complete epicranial arms and dorsal position of the antennariae, and lack a corpotentorium, except the Cleridae and the Corynetidae, represented by Trichodes and Necrobia respectively. All possess a complete gula except the latter genera and Collops, the representative of the Melyridae. This superfamily can be divided into three subgroups. One group will include the Lycidae and Lampyridae, characterized by a globular head, short broad gula, and absence of the pretentorinae. A second group will include the Phenodidae and the Cantharidae, characterized by a longer and flatter head and longer gula. The third group will include the Cleridae and the Corynetidae, possessing short incomplete arms, incomplete gular sutures, and a well-developed corpotentorium. Collops does not seem to fit in very well anywhere, though this genus, through the form of its dorsal surface and tentorium may possibly lean towards the second group. Cantharis of the second group, is peculiar in possessing a normal gula, whereas in the other forms the gula is rudimentary, though in all other

respects this genus is like the other members of this group. The first and second groups are no doubt closely related. The latter is probably the more generalized, possessing a dorsal surface resembling to a marked extent the dorsal surface of the Carabidae. The gula, in so far as it is complete, also resembles the condition of this structure in the families of the Adephaga, and particularly in *Necrophorus*, of the Silphoidea. It has, however, developed much farther, even, than in *Necrophorus*, being not only invaginated, but reduced to a more or less rudimentary state. The first group probably evolved from the second by the change in the shape of the head, due to the enormous development of the compound eyes and the loss of much of the gular region, which has probably fused with the cervix. Parallel with these changes, the pretentoria shifted their position so that they could better support the globular head, and came to assume the direction ordinarily assumed by the supratentoria of other genera. The third group would appear to be more closely related to the Mordelloidea than to this superfamily. The condition of the epicranial suture, the position of the antennariae, pretentorinae, and metatentorinae, the degree of development of the gula and tentorium, would all favor this assumption.

Cupesoidae.-- The representative of the Cupesidae studied does not show any particular peculiarities of structure of the head that would entitle it to be placed in a separate superfamily. It can be very readily included with the Mordelloidea, for approximately the same reasons as the Cleridae and Corynetidae.

Mordelloidea.-- The genera of the Mordelloidea show considerable homogeneity. Most of them possess heads that are elongate, with a generalized dorsal surface and a large postclypeus and labrum, both

on the same general level with the rest of the dorsal surface. The epicranial suture, however, shows considerable instability, sometimes showing complete arms and stem, as in *Epicauta*, while in others the epicranial suture may be extremely reduced, as in *Macrosiagon*. If these two genera are at all related, the condition of the epicranial suture can hardly throw any light on the degree of relationship. On the other hand, the metatentorinae are stable in position, and are located almost uniformly about half-way between the occipital foramen and the submentum. Another characteristic feature is the fact that most of the genera possess heads that are distinctly constricted at their caudal ends to form a neck. The Oedemeridae, the Cephaloidea, the Pyrochroidae, the Pedilidae, the Anthicidae, and possibly the Cupesidae and Meloidae, seem particularly closely related, through the possession of similarly shaped heads, whose caudal ends are distinctly constricted, of a generalized dorsal surface, of compound eyes that are usually more or less emarginated, of a ventral surface whose structures are practically in a similar condition, and of a tentorium that is alike throughout, with the exception of the Meloidae, in which the corpotentorium is absent. Though the dorsal surface of the Mordelloidea resembles to a considerable extent that of such families as the Carabidae and Cantharidae, yet this surface differs so widely in closely related groups that we can hardly place too much importance on the resemblance here. What seems to be far more important is the totally different condition of the ventral surfaces in the Mordelloidea and the Carabidae, for instance. In the former the gular sutures and the metatentorinae extend uniformly half way between the occipital foramen and the submentum; in the Carabidae the gular sutures extend the whole distance between these

parts, and the metatentorinae nearly to the submentum. The Mordelloidea and such groups as the Adephaga and Hydrophiloidea do not appear to be nearly related.

Elateroidea.-- The members of this superfamily are homogeneous with the exception of the Buprestidae. The pretentorinae and the antennariae are located on the dorsal surface, and the epicranial arms extend no farther caudad than the pretentorinae. On the ventral aspect, the metatentorinae extend but little cephalad of the occipital foramen, and the gular sutures no farther. The corpotentorium is lacking in all. In the Buprestidae, on the other hand, the pretentorinae and antennariae have migrated distinctly ventrad, and are not visible at all from the dorsal surface. The gular sutures extend the whole distance between the occipital foramen and the submentum, and there is a distinct corpotentorium. The Buprestidae are hardly closely related to the rest of the Elateroidea.

Dryopoidea.-- With the exception of the Georyssidae, the members of the Dryopoidea appear to be fairly homogeneous. The chief characteristics are very prominent widely separated metatentorinae, located very near the occipital foramen, and a very broad submentum. The ventral surface of the Georyssidae, as represented by Georyssus, is totally different. In this family the gular sutures extend nearly to the submentum, and are confluent through practically their entire extent. The metatentorinae cannot be definitely located. Georyssus would appear to be related to Hister, both through the condition of the gula, of the tentorium, and of the dorsal surface. The general appearance of the ventral surface in the Dryopoidea is much like that of the Elateroidea, and in other characteristics they are not unlike. These two superfamilies appear to be related.

Dascilloidea.-- The two representatives of two of the families of the Dascilloidea studied are similar in structure. There are no outstanding features that would warrant placing them in a separate superfamily. They are negative enough in their characteristics to fit in, perhaps, in a number of other superfamilies, such as the Mor-delloidea, Cucujoidea, and Tenebrionoidea.

Byrrnoidea.-- The representatives of the Dermestidae and the Byrrnidae studied, Dermestes and Byrrhus, do not seem to differ decidedly from one another, but the Nosodendronidae, represented by Nosodendron, may fit in better in some other group, such as the Dryopoidea. They resemble the members of this latter group in the position of the metatentorinae and in the form of the submentum. In Nosodendron, the metatentorinae are almost adjacent to the occipital foramen, with a membranous area included between them. That part of the metatentorium surrounding the periphery of the occipital foramen projects deep into the head. The supratentoria are well developed. None of these characteristics are possessed by the other two genera studied.

Rhysodoidea.-- The representative of this family studied, Rhysodes, shows distinct peculiarities in the structure of its head, such as an extremely thick chitinous head-wall, a fibrous condition of the cervix, an arrow-shaped head, enormously developed submentum, and very small mouth-parts. Its relationships are not at all clear.

Cucujoidea.-- The members of the Cucujoidea show on the whole a short broad head-capsule, a distinct ventral migration of the antennariae and protentorinae, the degeneration of the epicranial arms, and a slight migration of the metatentorinae from the occipital foramen. There is some variation in the dorsal aspect. The genera

belonging to the Mycetopharidae, the Mycetacidae, the Melanophthalmidae, the Endomychidae, and perhaps those of a few other families, possess dorsal surfaces that strongly resemble the dorsal surface of the Mordelloidea. In *Derodontus* and *Philothermus*, a colydiid, the antennariae and the pretentorinae are both on the dorsal aspect, located considerably caudad. The ventral aspect of all the members of the group, however, is strikingly similar. The tentorium is fairly uniform throughout the group except in *Tenebroidea* and *Phalacrus*, in which the pretentorium has distinctly degenerated, due probably to the heavy chitinization of the head wall. In the shape of the head and the condition of the metatentorinae and the gular sutures, the Cucujoides show a similarity to the Mordelloidea, and to the superfamily Tenebrionoidea.

Tenebrionoidea.-- There are no particular characteristics of the head-capsule that would separate this superfamily from the typical Mordelloidea. For instance, the dorsal and ventral surfaces and the endoskeleton of *Arthromacra*, *Pseudocistela*, and *Penthe*, are almost exactly like these parts of such genera of the Mordelloidea as *Epicauta*, *Cephaloon*, and *Macratria*. The corpotentorium of *Arthromacra* and *Epicauta* is, however, lacking.

Bostrichnoidea.--The structure of the various parts of the head-capsule of the representatives of the Bostrichoides varies considerably. The epicranial arms are complete in *Bostrichus*, *Lyctus*, *Flessicis*, and *Sphindus*. With the exception of *Sphindus* these families show a distinct ventral migration of the antennariae and pretentorinae. In contrast, *Ptinus* and *Sitodrepa* do not possess complete arms, and the antennariae and pretentorinae are located more dorsad, markedly so in the former. On the ventral surface, there is consid-

erable variation in the position of the metatentorinae. The tentorium also varies a great deal. This is probably not a very homogeneous group. *Sphindus* seems to be more structurally similar to *Sphaerius* than any other genus studied.

Scarabaeoidea.-- This is a very homogeneous group, characterized by a heavy chitinization of the head-wall, degeneration of the epicranial suture, ventral migration of the antennariae and the pretentorinae, and a complete gula, except in *Pseudolucanus*, in which the gular sutures extend no more than half the distance between the occipital foramen and the submentum. In the development of the ventral surface and perhaps the tentorium, the Scarabaeoidea should be classed with the Adephaga and related groups.

Cerambycoidea.-- This is also a very homogeneous group, characterized by a weak chitinization of the head wall, a distinct dorsal position of the antennariae and the pretentorinae, and a more or less well-developed epicranial suture. The gular sutures are generally short. The tentorium is delicate and membranous throughout.

Rhynchophora.-- The members of this group may or may not possess a snout. They may or may not possess confluent gular sutures. When they do, the condition is the same as in other Coleoptera. They may or may not possess a labrum. There is no definite character of the head-capsule by which the Rhynchophora can be separated from other Coleoptera. The affinities of this group are not at all clear.

Conclusions.-- The condition of the dorsal surface throughout the groups is most variable, and can be relied upon but little to furnish evidence of the degree of relationship. On the ventral surface the condition is much more stable, and probably much more reliable in indicating affinities. The tentorium is less variable than

the dorsal surface, and less stable than the ventral surface. Weighing the evidence presented in this study, two large groups of most of the families can be made. The Cupesoides, the Mordellicides, the Elateroidea, the Dryopoidea, the Dascilloidea, the Byrrhoidea, the Cucujoidea, the Tenebrionoidea, and the Bostrichoidea should probably be grouped together, while the characteristic families of the Cantharoidea, the Staphylinidea, and the Silphoidea should perhaps be grouped with the Adephaga and Hydrophilidea. The Scarabaeoidea may also be included in this latter group. The affinities of the Cerambycoidea and the Rhynchophora are too vague to include either in the two larger groups.

VI. SUMMARY

1. This investigation deals with the homology of all the structures of the head-capsule of one or more representatives of ninety-four of the one hundred and nine families of Coleoptera listed by Leng in his recent catalogue. One hundred and fifty-five genera, of which one hundred and thirty have been figured, nearly all representing different important subgroups, have been studied.

2. This serial study has made it possible to identify the same structures in a wide series of forms, and to definitely fix the homology of all the parts of the head-capsule.

3. Hypothetical types have been constructed, based on the structure of the head-capsule of generalized insects and Coleoptera. These show the Coleoptera to have developed in general a consolidation of sclerites and a heavier chitinization of the wall of the head, a compacting of the head as a whole, and an approximation of the dorsal and ventral movable parts at the cephalic end.

4. The epicranial suture has been identified in all but two

of the genera studied. It has proved a great aid in determining the limits of neighboring parts. What may appear to be a distinct epicranial suture may not even be a suture. It is sometimes distinctly invaginated. Its identity can only be definitely fixed by determining the location of the pretentorinae, which are always associated with it.

5. The limits of the vertex are dependent upon the position of the epicranial suture. In the Rhynchophora nearly all of the snout belongs to the vertex.

6. The unmodified occipital suture has been identified only in the Adephaga. The cephalic end of it on the ventral surface is always represented by part of a curving ridge, which is present in all but a few genera.

7. The supratentorinae have been identified in a few genera, nearly all of which belong to the Staphylinoidae.

8. The pretentorinae are the great landmarks of the head-capsule and have been identified in all but two genera. They are, in the vast majority of genera, located near the cephalic end of the epicranial arms. A definite determination of the pretentorinae cannot always be made without an ental examination of the head.

9. The size and form of the front is dependent upon the position of the epicranial arms. In the Cerambycoidea it is large. In many genera, as illustrated by *Omophron*, *Harpalus*, and *Tachinus*, it is partly or wholly invaginated. It may probably be rudimentary or wholly lost in many genera in which the mesal parts of the epicranial arms have disappeared.

10. What has been called the clypeal suture in such genera as *Cicindela* and *Harpalus* is not even a suture, but the line of invagi-

nation of the front.

11. The clypeus is always divided into the postclypeus and the preclypeus. The preclypeus is with one exception always distinctly membranous. It may be as large or larger than the labrum.

12. There is a distinct clypealia present in the Coleoptera, and in widely separated groups, such as the Alephaga and the Cerambycoidea.

13. The labrum may be indistinctly determined in both Rhyncho-phora and other Coleoptera. It may also be quite distinct in some Rhynchophora where it is considered to be absent.

14. The submentum is always located distinctly cephalad of the occipital foramen, with a chitinized area between it and the foramen.

15. The metatentorinae may be located on the cephalo-lateral border of the occipital foramen, as in generalized insects, or they may be far cephalad of this location.

16. All that region between the occipital foramen and the submentum is a part of the postgenae, produced by the fusion on the meson of the mesal margins of the postgenae.

17. The gular sutures result from the cephalic migration of the metatentorinae.

18. The gula is that area included between the gular sutures, and is, therefore, derived from the postgenae. The majority of the Coleoptera possess a gula that extends no more than half the distance between the occipital foramen and the submentum.

19. The tentorium of the Coleoptera is typically quite similar in form and development to that of generalized insects. Frequent modifications are loss of chitinization, loss of eopretentorium and laminatentorium. Occasionally the pretentorium may be rudimentary.

The functions of the absent parts are assumed by other parts of the tentorium, or by the pharynx, or the head may be so compact and chitinized that a tentorium is no longer needed.

20. The cephalic migration of the submentum, and the subsequent formation of an indistinguishable area between it and the occipital foramen is due either to the caudad migration of the occipital foramen, or to the cephalic pull on the mouth-parts, or to both. The cephalic migration of the metatentorium, and, therefore, the metatentorinae, with consequent production of the gula, is probably due to the cephalic pull on the tentorium to furnish a firmer support for the muscles and tendons of the mouth-parts.

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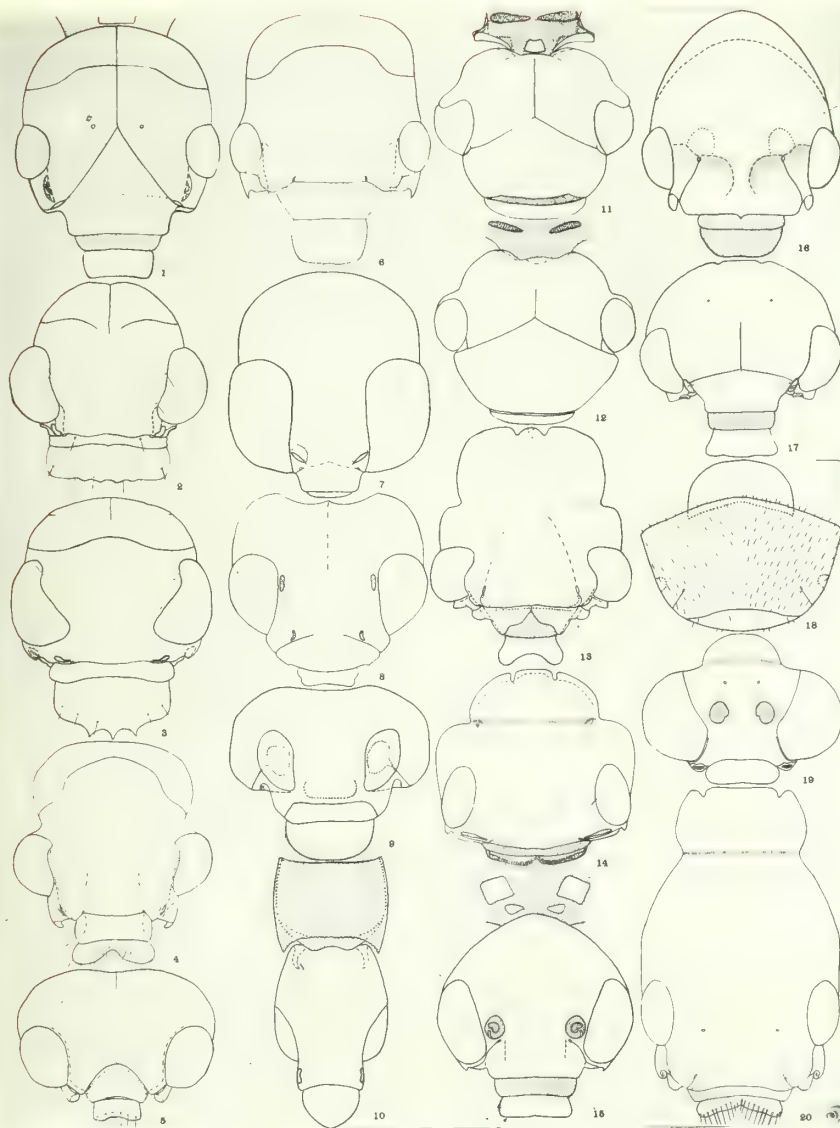
EXPLANATION OF PLATE I

Dorsal aspect of the head

Fig. 1. Hypothetical head.

2. *Tetracha carolina*.
3. *Cicindela formosa*.
4. *Calosoma calidum*.
5. *Omophron americanum*.
6. *Harpalus erraticus*.
7. *Peltodytes 12-punctatus*.
8. *Cybister fimbriolatus*.
9. *Dineutes assimilis*.
10. *Molamba lunata*.
11. *Hydrous triangularis*.
12. *Hydrophilus obtusatus*.
13. *Necrophorus carolina*.
14. *Creophilus villosus*.
15. *Aleochara lata*.
16. *Connophron fossiger*.
17. *Tachinus fimbriatus*.
18. *Leptinus testaceus*.
19. *Stenus flavicornis*.
20. *Gastrolobium bicolor*.

PLATE I

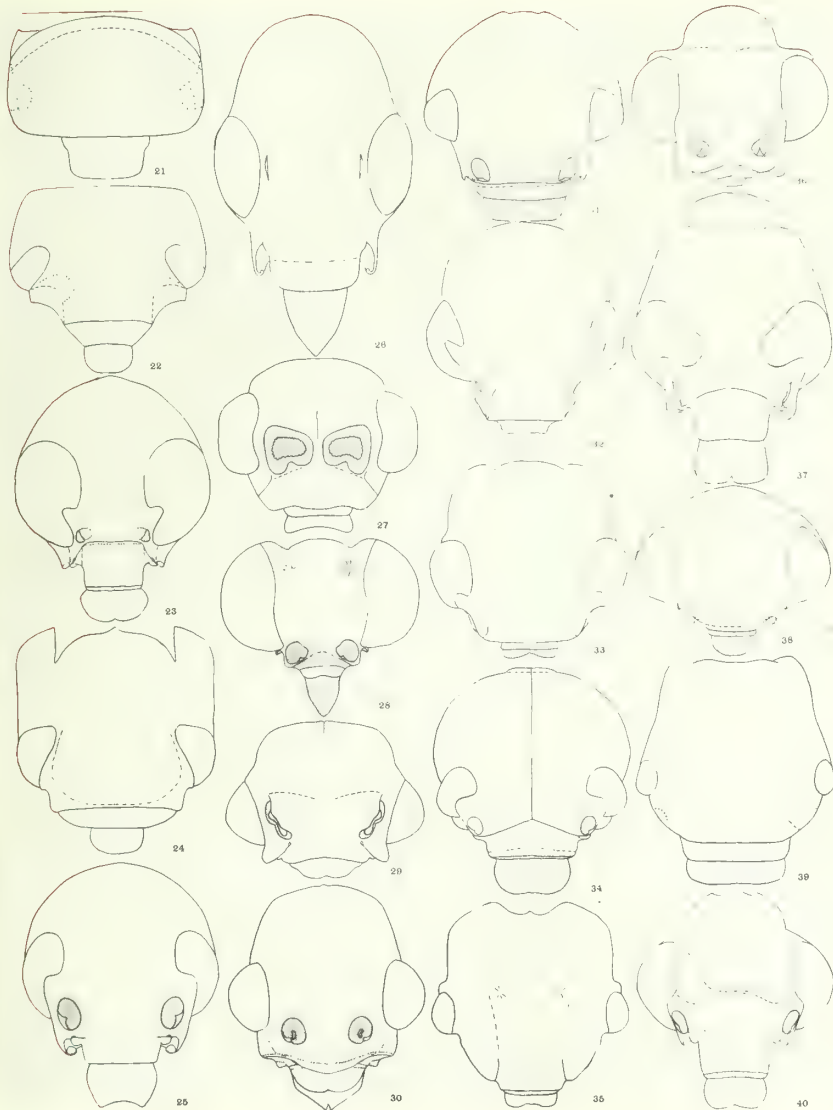


EXPLANATION OF PLATE II

Dorsal aspect of the head

- Fig. 21. *Limulodes paradoxus*.
22. *Sphaerius politus*.
23. *Scaphidium quadriguttatum*.
24. *Hister merdarius*.
25. *Nacerda melanura*.
26. *Macrosiagon dimidiatum*.
27. *Calopteron terminale*.
28. *Photinus pyralis*.
29. *Phengodes plumosa*.
30. *Chauliognathus pennsylvanicus*.
31. *Collops nigriceps*.
32. *Trichodes nuttali*.
33. *Necrobia rufipes*.
34. *Epicauta marginata*.
35. *Pytho americanus*.
36. *Cupes concolor*.
37. *Cephaloon lepturides*.
38. *Tomoxia bidentata*.
39. *Eurystethus debilis*.
40. *Neopyrochroa flabellata*.

PLATE II

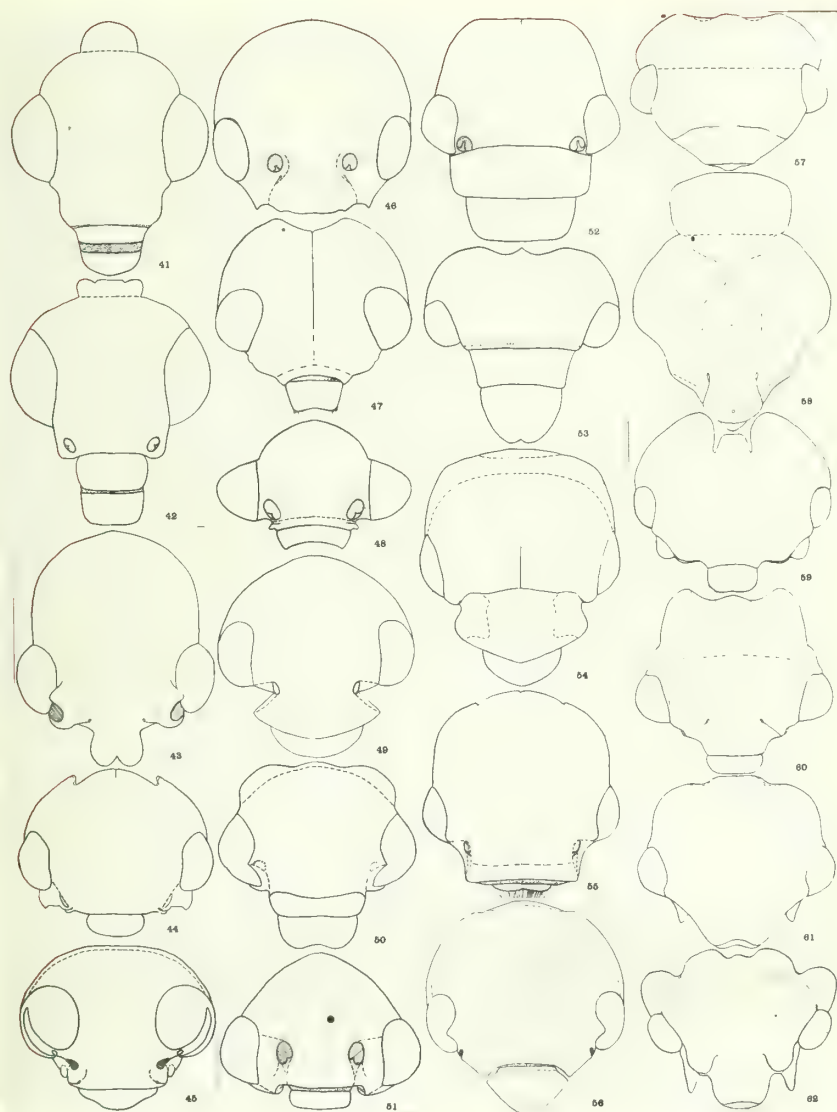


EXPLANATION OF PLATE III

Dorsal aspect of the head

- Fig. 41. *Macratrria murina*.
42. *Notoxus anchora*.
43. *Sandalus niger*.
44. *Alaus oculatus*.
45. *Throscus chevrolati*.
46. *Tharops ruficornis*.
47. *Chalcophora virginiensis*.
48. *Psephenus lecontei*.
49. *Helichus striatus*.
50. *Eucinetus morio*.
51. *Cyphon ruficollis*.
52. *Stenelmis sinuata*.
53. *Heterocerus undatus*.
54. *Georyssus californicus*.
55. *Dermestes lardarius*.
56. *Byrrhus americanus*.
57. *Nosodendron unicolor*.
58. *Rhysodes americanus*.
59. *Tenebroides sinuatus*.
60. *Phenolia grossa*.
61. *Glischrochilus quadriguttatus*.
62. *Cucujus clavipes*.

PLATE III



EXPLANATION OF PLATE IV

Dorsal aspect of the head

Fig. 63. *Phyconomus marinus*.

64. *Languria mozardi*.

65. *Megalodacne fasciata*.

66. *Derodontus maculatus*.

67. *Anchicera ephippiata*.

68. *Byturus unicolor*.

69. *Mycetophagus punctatus*.

70. *Philothermus glabriculus*.

71. *Phymaphora pulchella*.

72. *Phalacrus politus*.

73. *Alobates pennsylvanica*.

74. *Melanophthalma angularis*.

75. *Endomychus biguttatus*.

76. *Hippodamia convergens*.

77. *Arthromacra aenea*.

78. *Pseudocistela brevis*.

79. *Adalia bi-punctata*.

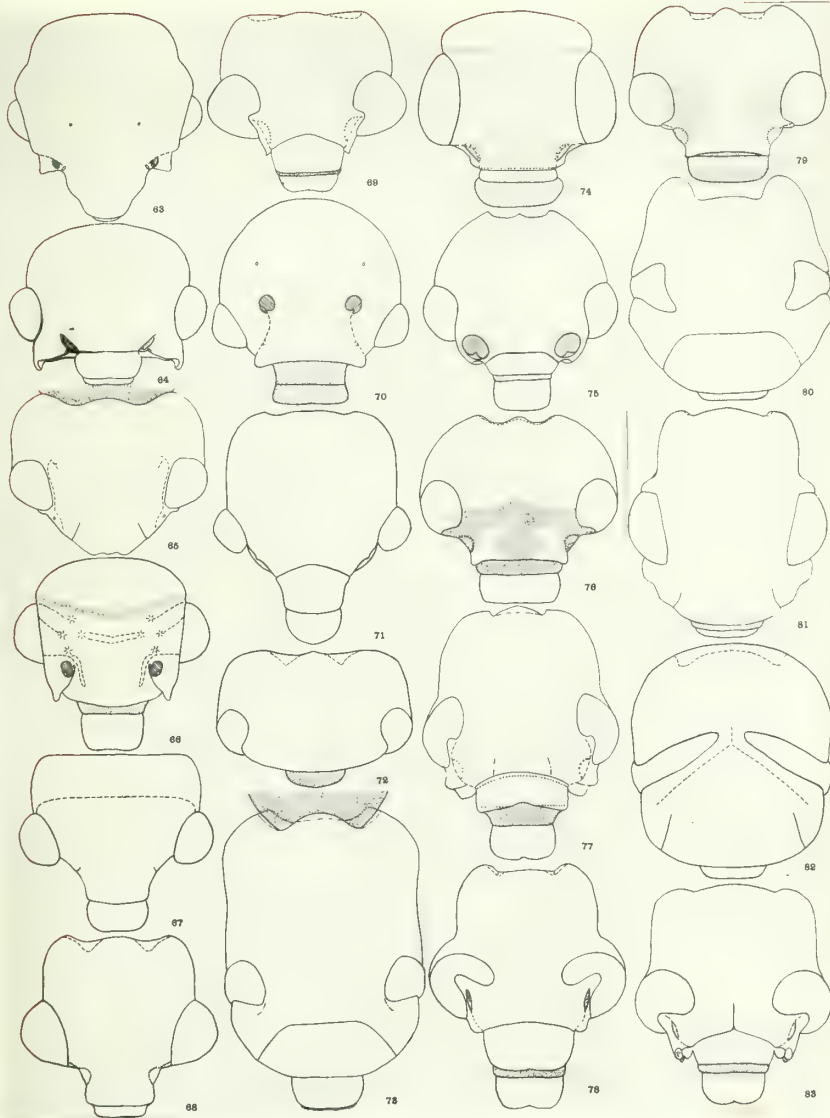
80. *Tenebrio molitor*.

81. *Boros unicolor*.

82. *Hyporphagus* sp.

83. *Penthe obliquata*.

PLATE IV



EXPLANATION OF PLATE V

Dorsal aspect of the head

Fig. 84. *Ptinus brunneus*.

85. *Sitodrepa panicæa*.

86. *Bostrichus bicornis*.

87. *Lyctus planicollis*.

88. *Plesiocis cribrum*.

89. *Sphindus americanus*.

90. *Aphodius fimentarius*.

91. *Dichelonyx elongata*.

92. *Pelidnota punctata*.

93. *Strategus julianus*.

94. *Harpalus erraticus*,
longitudinal cross-section.

95. *Osmoderma eremicola*.

96. *Trox suberosus*.

97. *Pseudolucanus dama*.

98. *Passalus cornuta*.

99. *Syneta ferruginea*.

100. *Derobrachus brunneus*.

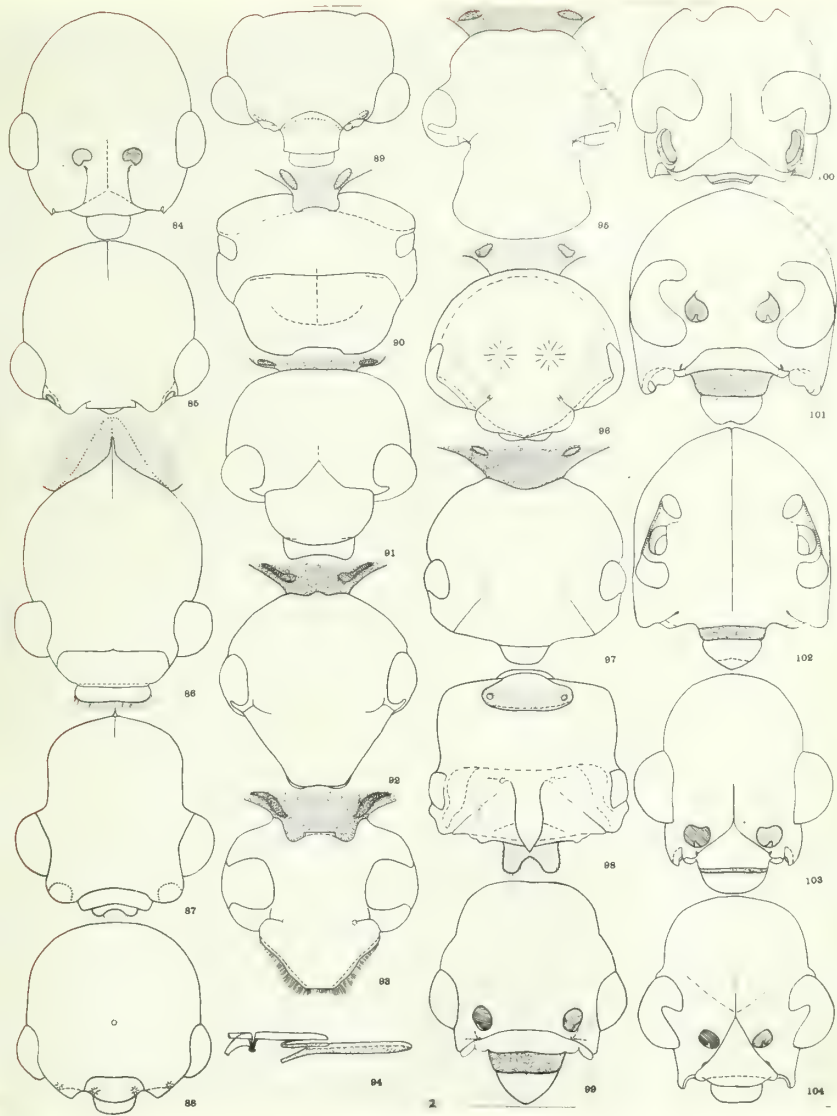
101. *Glycobius speciosus*.

102. *Tetraopes tetraophthalmus*.

103. *Donacia piscatrix*.

104. *Crioceris asparagi*.

PLATE V



EXPLANATION OF PLATE VI

Dorsal aspect of the head

Fig. 105. *Parandra brunnea*.

106. *Cryptocephalus quadruplex*.

107. *Chrysochus auratus*.

108. *Leptinotarsa decimlineata*.

109. *Eupsalis minuta*.

110. *Blepharida rhois*.

111. *Anoplitis nervosa*.

112. *Chelymorpha argus*.

113. *Pachymerus arthriticus*.

114. *Diabrotica 12-punctata*.

115. *Eurymycter fasciatus*.

116. *Epicaerus imbricatus*.

117. *Rhynchites bicolor*.

118. *Dendroctonus valens*.

119. *Thecesternus humeralis*.

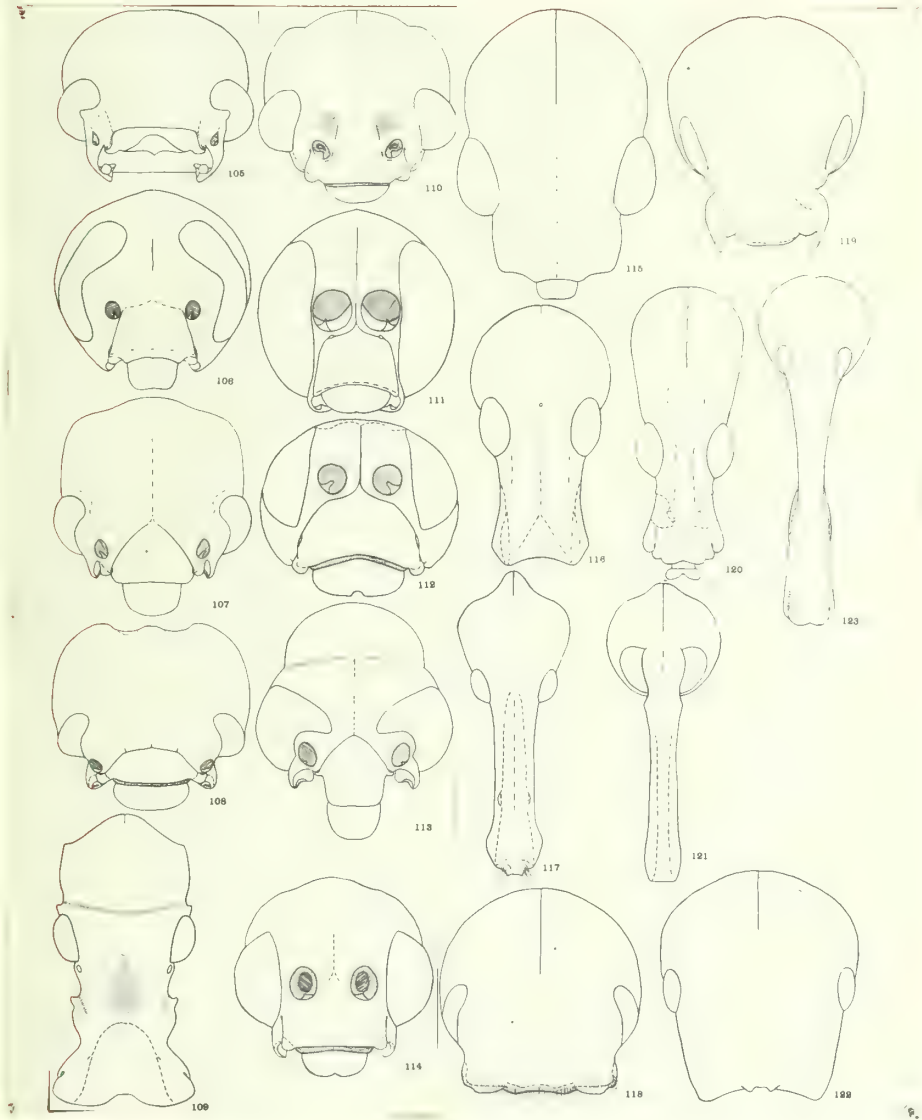
120. *Attelabus analis*.

121. *Sphenophorus aequalis*

122. *Scolytus quadrispinosus*.

123. *Lixus macer*.

PLATE VI



EXPLANATION OF PLATE VII

Lateral aspect of the head

Fig. 124. *Tetracha carolina*.

125. *Cicindela formosa*.

126. *Calosoma calidum*.

127. *Omophron americanum*.

128. *Peltodytes 12-punctatus*.

129. *Harpalus erraticus*.

130. *Cybister fimbriolatus*.

131. *Hydrous triangularis*.

132. *Hydrophilus obtusatus*.

133. *Leptinus testaceus*.

134. *Necrophorus carolina*.

135. *Dineutes assimilis*.

136. *Connophron fossiger*.

137. *Molamba lunata*.

138. *Stenus flavicornis*.

139. *Gastrolobium bicolor*.

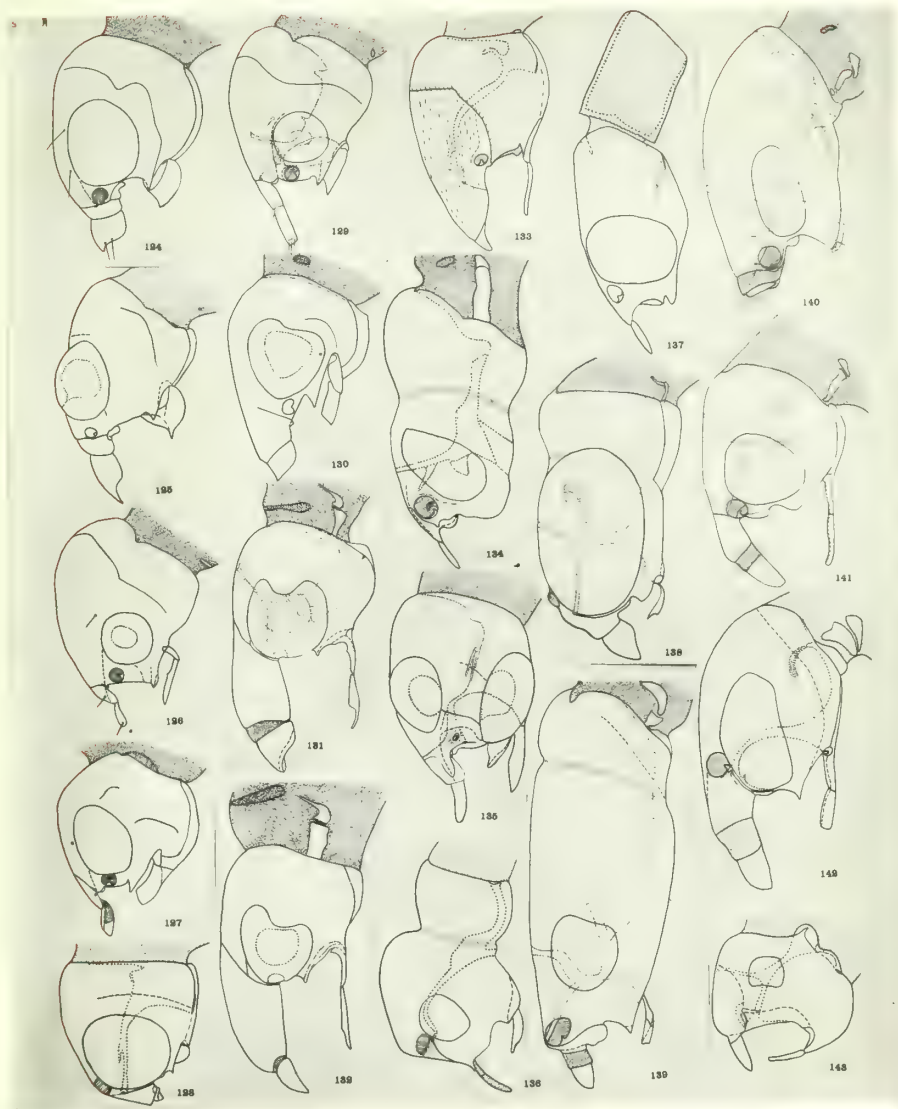
140. *Creophilus villosus*.

141. *Tachinus fimbriatus*.

142. *Aleochara lata*.

143. *Limulodes paradoxus*.

PLATE VII



EXPLANATION OF PLATE VIII

Lateral aspect of the head

Fig. 144. *Sphaerius politus*.

145. *Scaphidium quadriguttatum*.

146. *Chauliognathus pennsylvanicus*,
cross-section showing invagination
of part of the gula.

147. *Hister merdarius*.

148. *Photinus pyralis*.

149. *Calopteron terminale*.

150. *Phengodes plumosa*.

151. *Chauliognathus pennsylvanicus*.

152. *Collops nigriceps*.

153. *Trichodes nuttali*.

154. *Necrobia rufipes*.

155. *Cupes concolor*.

156. *Cephaloon lepturides*.

157. *Nacerda melanura*.

158. *Tomoxia bidentata*.

159. *Macrosiagon dimidiatum*.

160. *Epicauta marginata*.

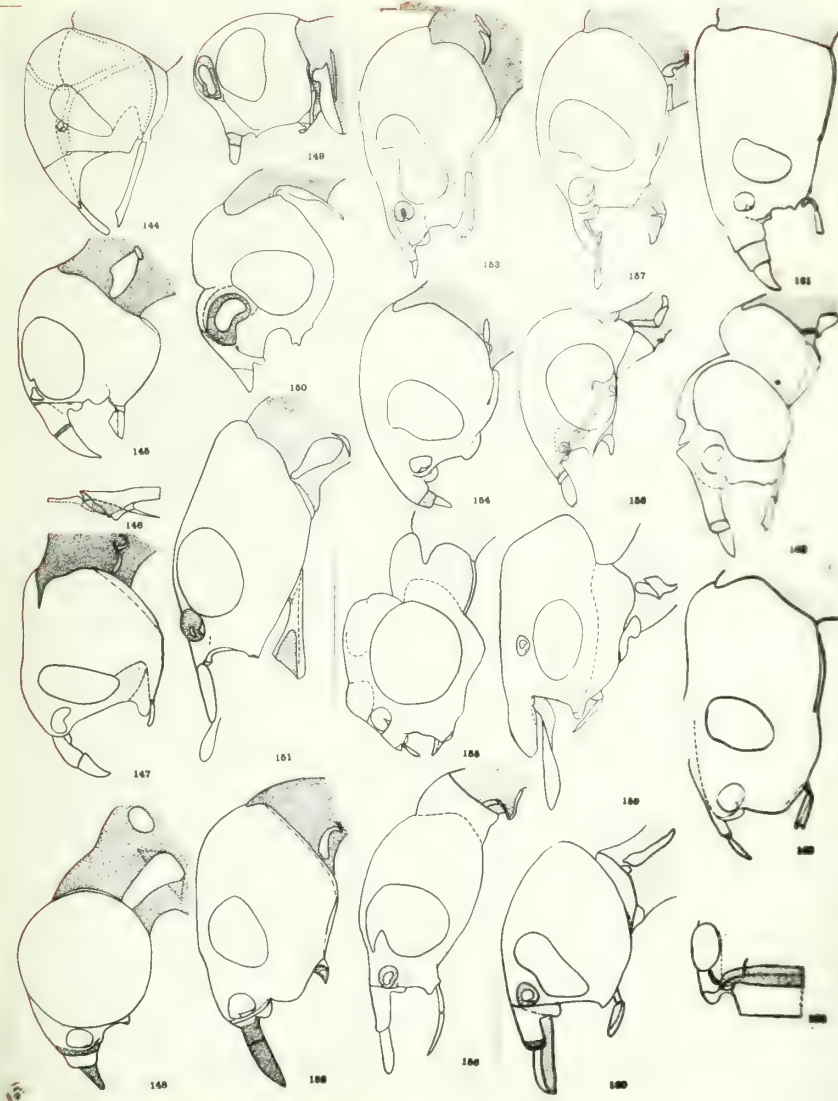
161. *Eurystethus debilis*.

162. *Neopyrochroa flabellata*.

163. *Pytho americanus*.

164. *Harpalus erraticus*,
dorsal aspect, showing invagination
associated with epicranial suture.

PLATE VIII

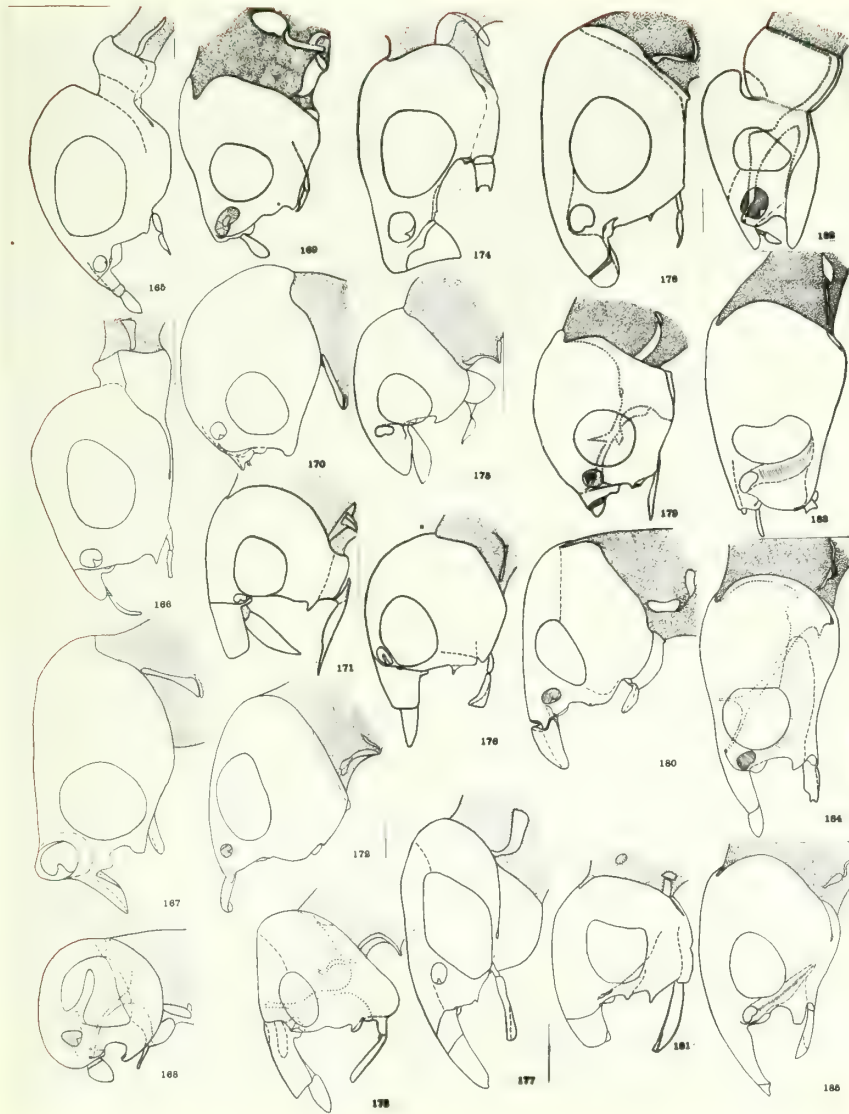


EXPLANATION OF PLATE IX

Lateral aspect of the head

- Fig. 165. *Macratris murina*.
166. *Notoxus anchora*.
167. *Sandalus niger*.
168. *Throscus chevrolati*.
169. *Alaus oculatus*.
170. *Tharops ruficornis*.
171. *Heterocerus undatus*.
172. *Chalcophora virginiensis*.
173. *Georyssus californicus*.
174. *Psephenus lecontei*.
175. *Helichus striatus*.
176. *Stenelmis sinuata*.
177. *Eucinetus morio*.
178. *Cyphon ruficollis*.
179. *Dermestes lardarius*.
180. *Byrrhus americanus*.
181. *Nosodendron unicolor*.
182. *Rhysodes americanus*.
183. *Tenebroides sinuatus*.
184. *Phenolia grossa*.
185. *Glischrochilus quadriguttatus*.

PLATE IX



EXPLANATION OF PLATE X

Lateral aspect of the head

Fig. 186. *Phyconomus marinus*.

187. *Cucujus clavipes*.

188. *Languria mozardi*.

189. *Megalodacne fasciata*.

190. *Anchicera ehippiata*.

191. *Byturus unicolor*.

192. *Mycetophagus punctatus*.

193. *Derodontus asculatus*.

194. *Philothermus glabriculus*.

195. *Melanophthalma angularis*.

196. *Phymaphora pulchella*.

197. *Endomychus biguttatus*.

198. *Phalacrus politus*.

199. *Hippodamia convergens*.

200. *Adalia bi-punctata*.

201. *Pseudocistela brevis*.

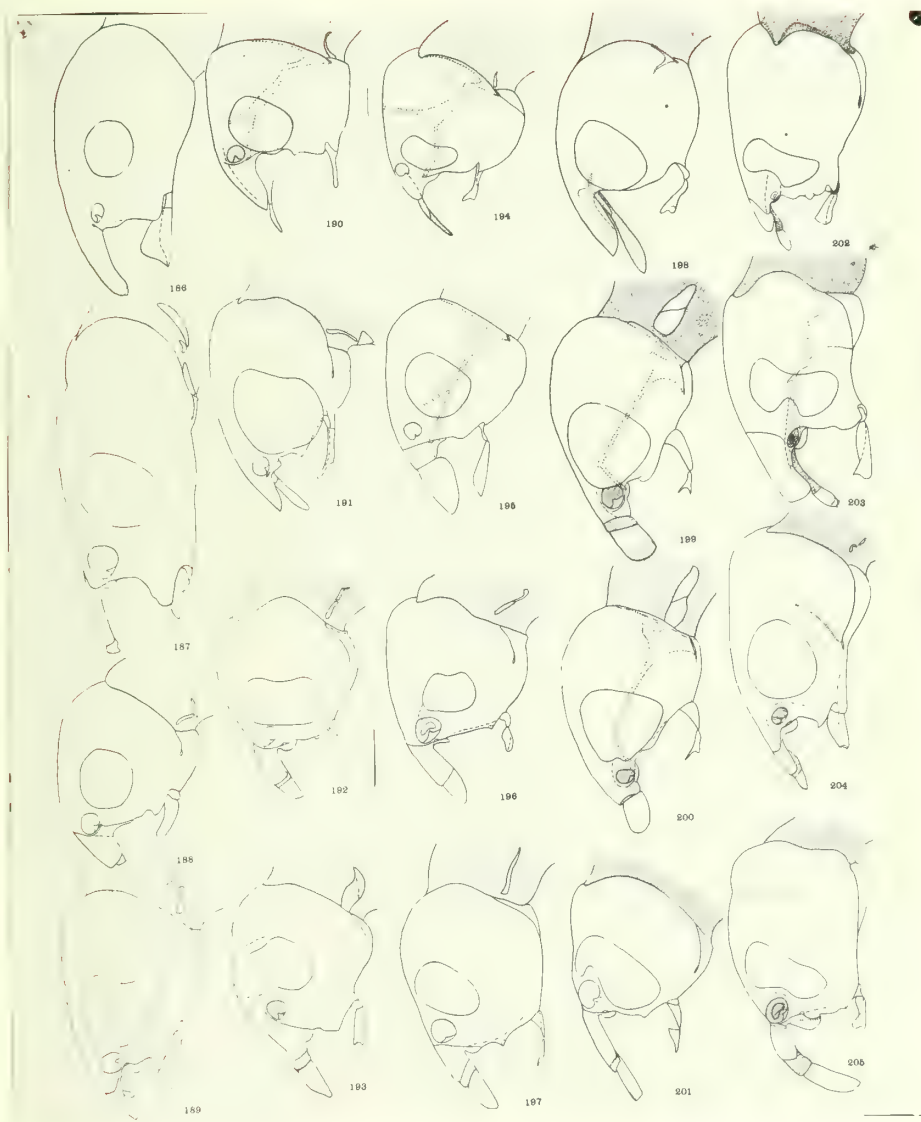
202. *Alobates pennsylvanica*.

203. *Tenebrio molitor*.

204. *Boros unicolor*.

205. *Arthromacra aenea*.

PLATE X



EXPLANATION OF PLATE XI

Lateral aspect of the head

Fig. 206. *Hyporhagus* sp.

207. *Penthe obliquata*.

208. *Ptinus brunneus*.

209. *Sitodrepa panicea*.

210. *Lyctus planicollis*.

211. *Bostrichus bicornis*.

212. *Sphindus americanus*.

213. *Plesiocis cribrum*.

214. *Aphodius fimetarius*.

215. *Dichelonyx elongata*.

216. *Pelidnota punctata*.

217. *Strategus julianus*.

218. *Osmoderma eremicola*.

219. *Trox suberosus*.

220. *Pseudolucanus dama*.

221. *Passalus cornuta*.

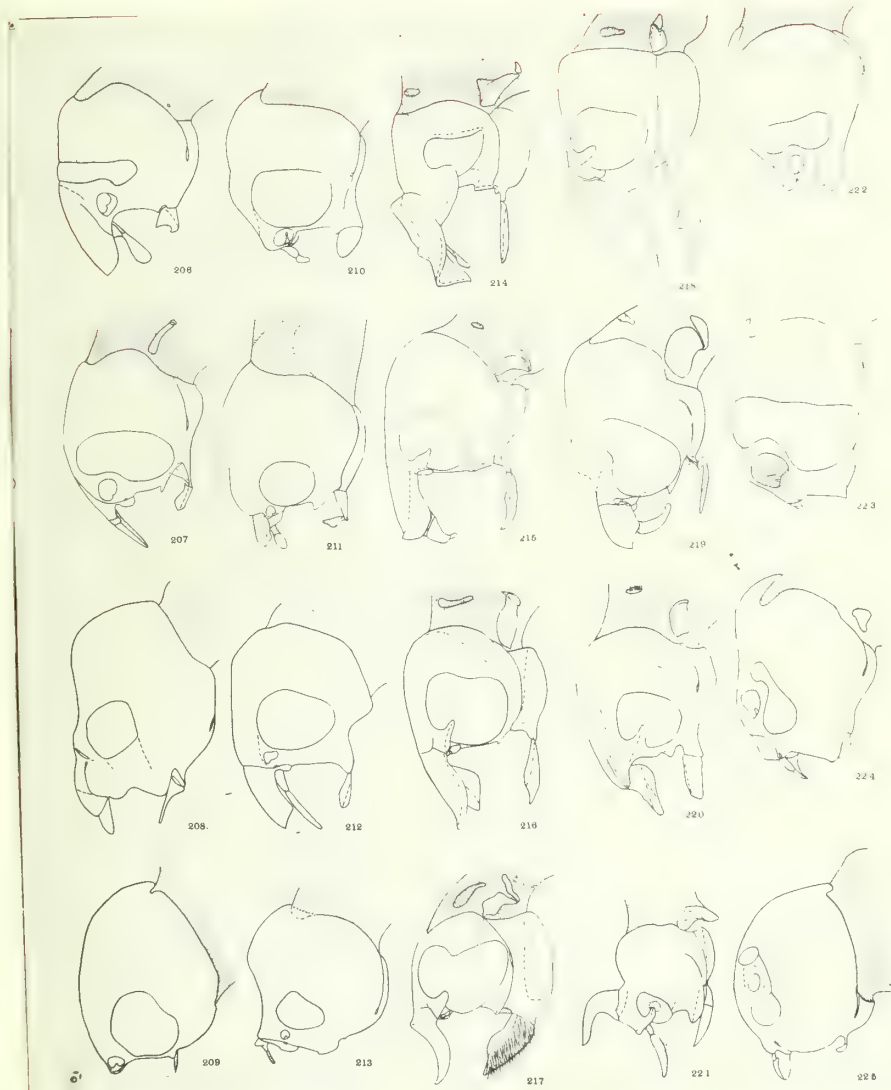
222. *Parandra brunnea*.

223. *Derobrachus brunneus*.

224. *Glycobius speciosus*.

225. *Tetraopes tetraophthalmus*.

PLATE XI



EXPLANATION OF PLATE XII

Lateral aspect of the head

Fig. 226. *Donacia piscatrix*.

227. *Syneta ferruginea*.

228. *Criocerus asparagi*.

229. *Cryptocephalus quadruplex*.

230. *Chrysochus auratus*.

231. *Leptinotarsus decimlineata*.

232. *Diabrotica 12-punctata*.

233. *Blepharida rhois*.

234. *Anoplitis nervosa*.

235. *Chelymorpha argus*.

236. *Pachymerus arthriticus*.

237. *Eupsalis minuta*.

238. *Eurymycter fasciatus*.

239. *Rhynchites bicolor*.

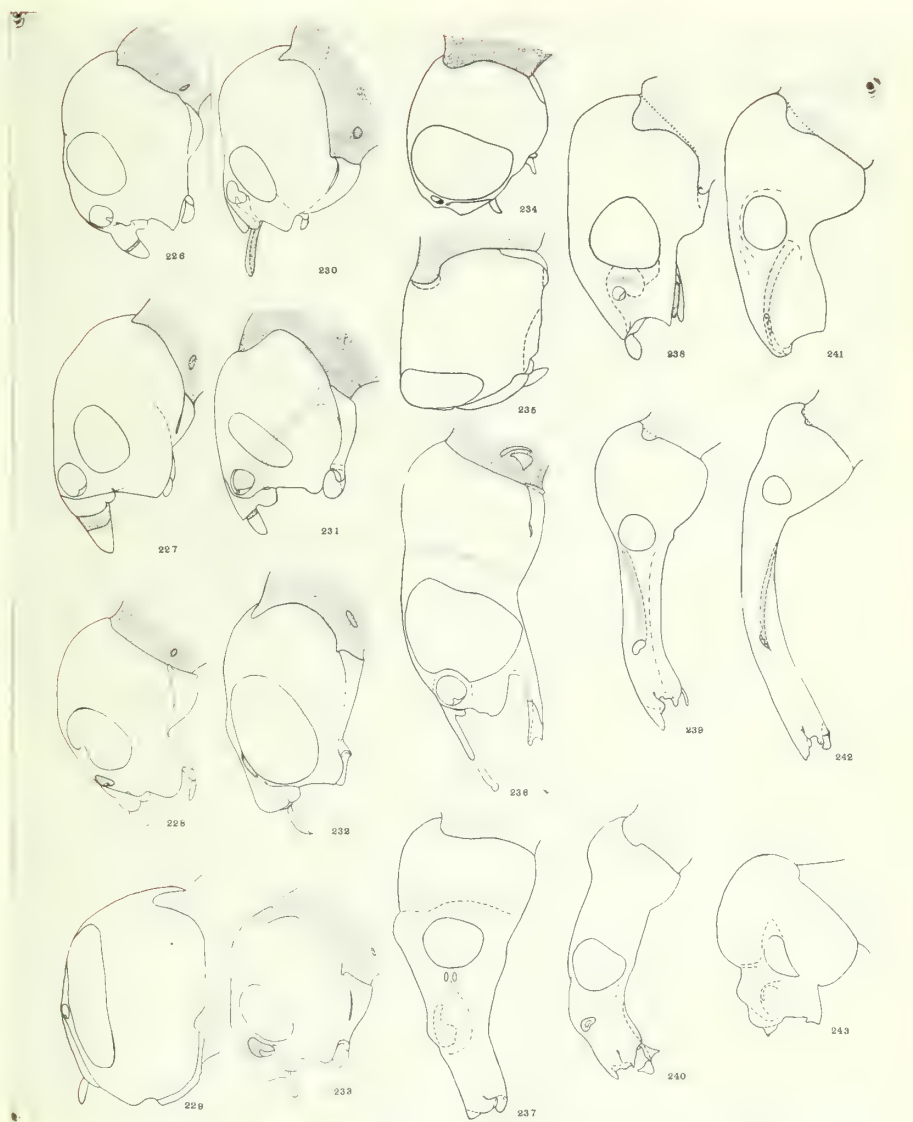
240. *Attelabus analis*.

241. *Epicaerus imbricatus*.

242. *Lixus macer*.

243. *Thecesternus humeralis*.

PLATE XII



EXPLANATION OF PLATE XIII

Lateral aspect of the head

Fig. 244. *Sphenophorus aequalis*.

245. *Scolytus quadrispinosus*.

246. *Dendroctonus valens*.

Ventral aspect of the head

Fig. 247. Hypothetical head.

248. *Tetracha carolina*.

249. *Cicindela formosa*.

250. *Calòsoma calidum*.

251. *Harpalus erraticus*.

252. *Omophron americanum*.

253. *Peltodytes 12-punctatus*.

254. *Cybister fimbriolatus*.

255. *Dineutes assimilis*.

256. *Hydrous triangularis*.

257. *Hydrophilus obtusatus*.

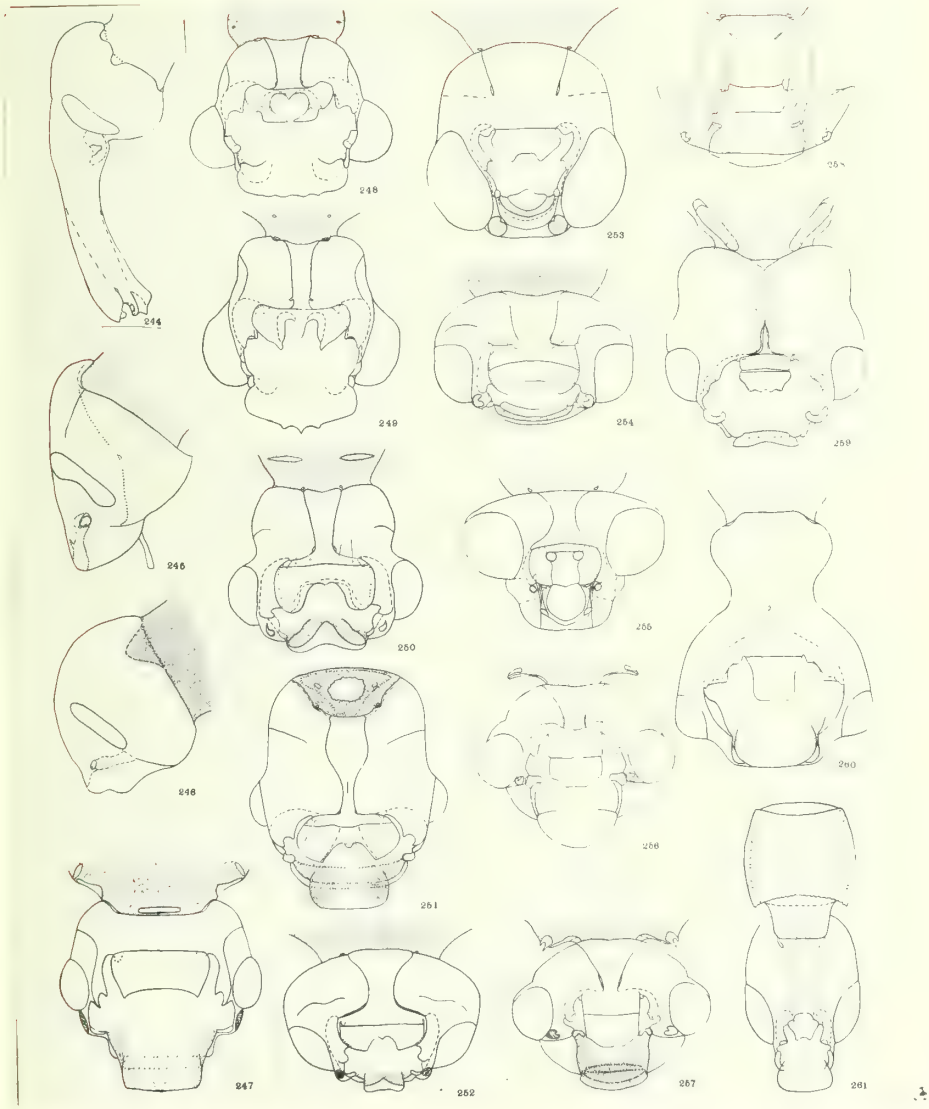
258. *Leptinus testaceus*.

259. *Necrophorus carolina*.

260. *Connophron fossiger*.

261. *Molamba lunata*.

PLATE XIII

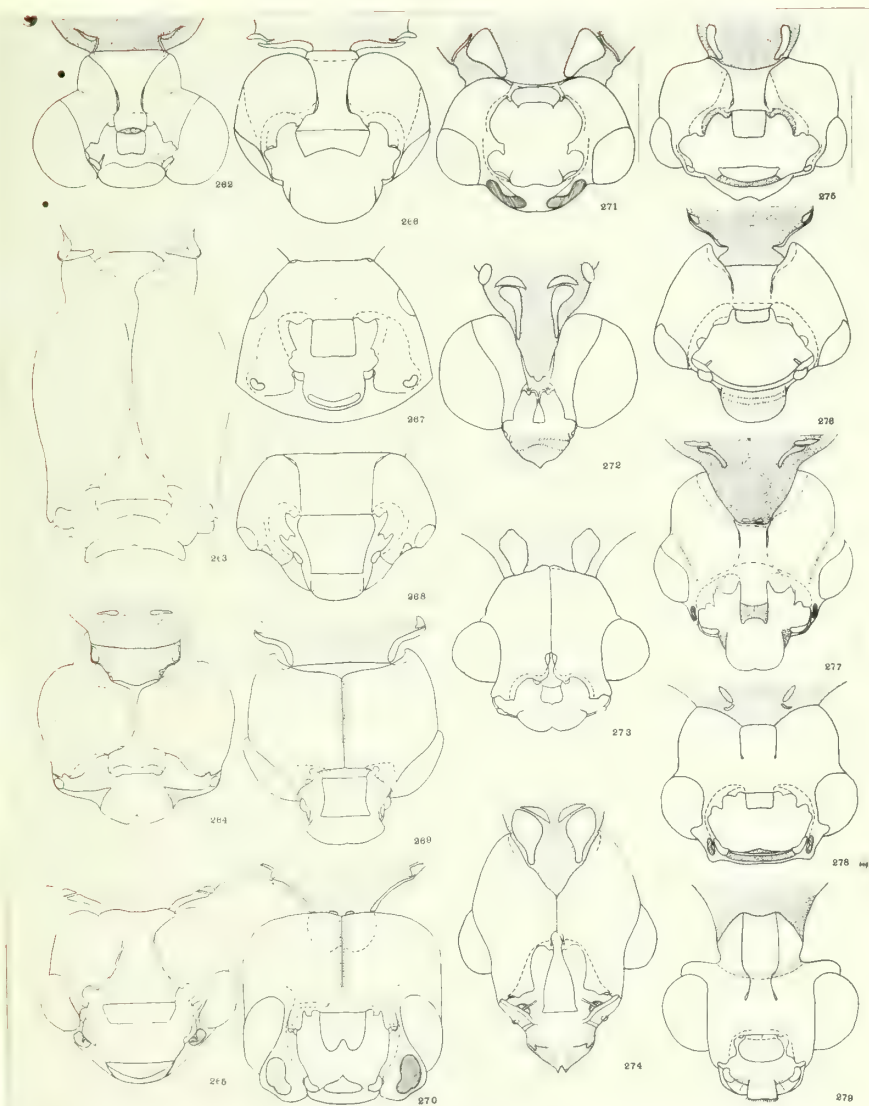


EXPLANATION OF PLATE XIV

Ventral aspect of the head

- Fig. 262. *Stenus flavicornis*.
263. *Gastrolobium bicolor*.
264. *Creophilus villosus*.
265. *Tachinus fimbriatus*.
266. *Aleochara lata*.
267. *Limulodes paradoxus*.
268. *Sphaerius politus*.
269. *Scaphidium quadriguttatum*.
270. *Hister merdarius*.
271. *Calopteron terminale*.
272. *Photinus pyralis*.
273. *Phengodes plumosa*.
274. *Chauliognathus pennsylvanicus*.
275. *Cantharis bilineatus*.
276. *Collops nigriceps*.
277. *Trichodes nuttali*.
278. *Necrobia rufipes*.
279. *Cupes concolor*.

PLATE XIV

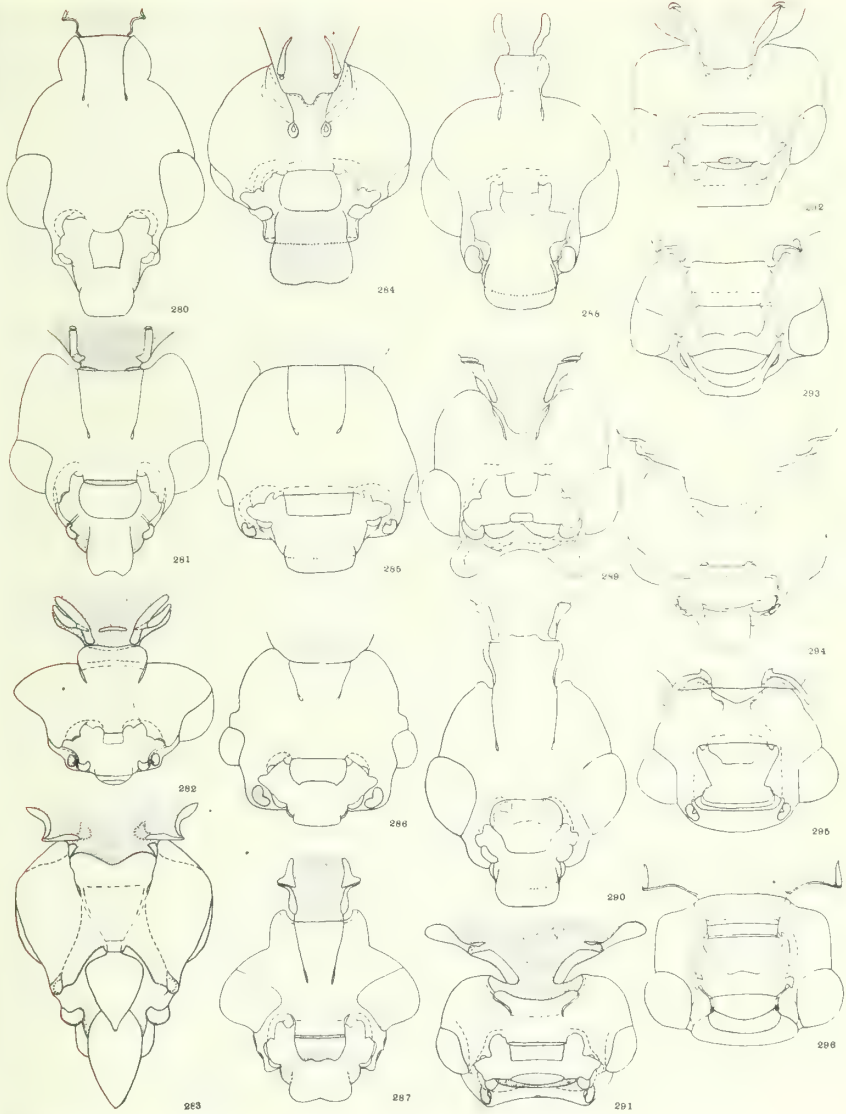


EXPLANATION OF PLATE XV

Ventral aspect of the head

- Fig. 280. *Cephaloon lepturides*.
281. *Nacerda melanura*.
282. *Tomoxia bidentata*.
283. *Macrosiagon dimidiatum*.
284. *Epicauta marginata*.
285. *Eurystethus debilis*.
286. *Pytho americanus*.
287. *Neopyrochroa flabellata*.
288. *Macratrria murina*.
289. *Sandalus niger*.
290. *Notoxus anchora*.
291. *Alaus oculatus*.
292. *Tharops ruficornis*.
293. *Throscus chevrolati*.
294. *Chalcophora virginienensis*.
295. *Psephenus lecontei*.
296. *Helichus striatus*.

PLATE XV

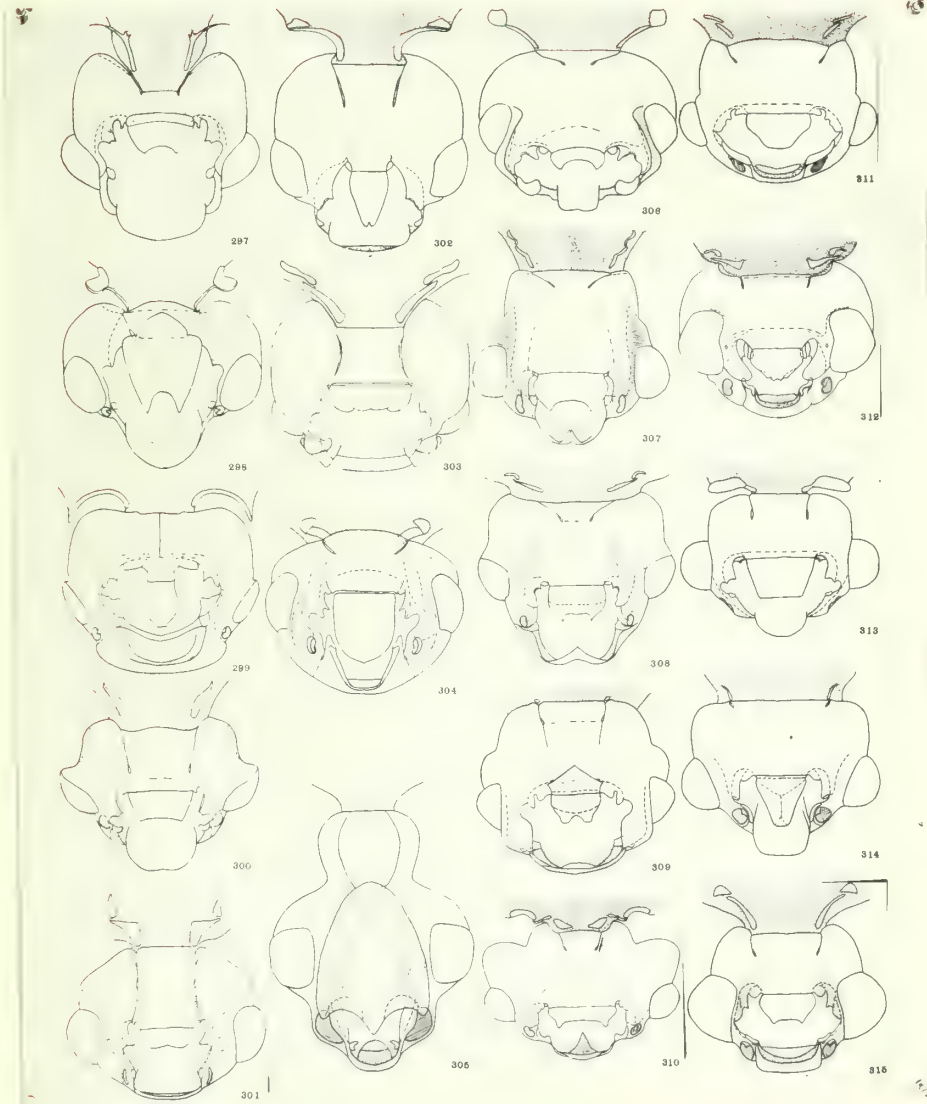


EXPLANATION OF PLATE XVI

Ventral aspect of the head

- Fig. 297. *Stenelmis sinuata*.
298. *Heterocerus undatus*.
299. *Georyssus californicus*.
300. *Encinetus morio*.
301. *Cyphon ruficollis*.
302. *Dermestes lardarius*.
303. *Byrrhus americanis*.
304. *Nosodendron unicolor*.
305. *Rhysodes americanum*.
306. *Tenebroides sinuatus*.
307. *Phenolia grossa*.
308. *Glischrochilus quadriguttatus*.
309. *Phyconomus marinus*.
310. *Cucujus clavipes*.
311. *Languria mozardi*.
312. *Megalodacne fasciata*.
313. *Derodontus maculatus*.
314. *Anchicera ehippiata*.
315. *Byturus unicolor*.

PLATE XVI



EXPLANATION OF PLATE XVII

Ventral aspect of the head.

Fig. 316. *Mycetophagus punctatus*.

317. *Philothermus glabriculus*.

318. *Melanophthalma angularis*.

319. *Phymaphora pulchella*.

320. *Endomychus biguttatus*.

321. *Phalacrus politus*.

322. *Hippodamia convergens*.

323. *Adalia bi-punctata*.

324. *Pseudocistela brevis*.

325. *Alobates pennsylvanica*.

326. *Tenebrio molitor*.

327. *Boros unicolor*.

328. *Arthromacra aenea*.

329. *Hyporphagus* sp.

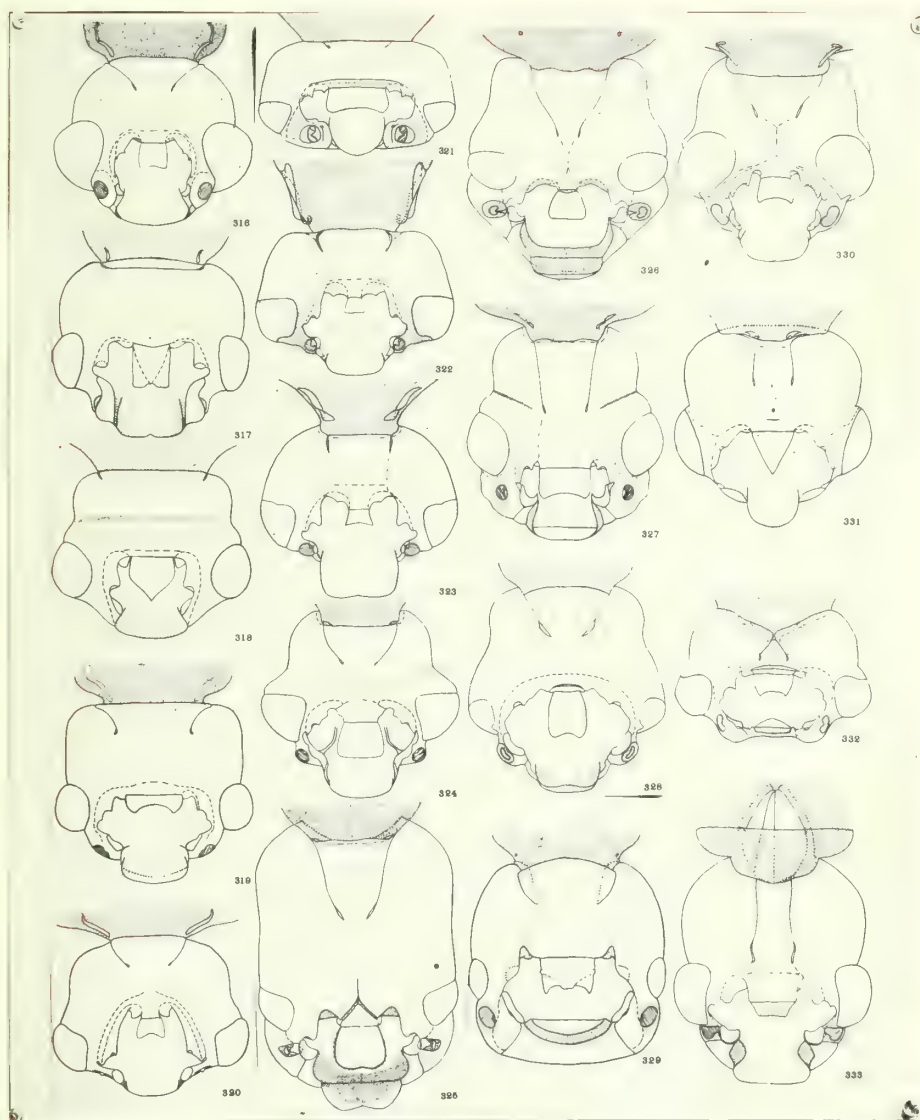
330. *Penthe obliquata*.

331. *Ptinus brunneus*.

332. *Sitodrepa panicea*.

333. *Bostrichus bicornis*.

PLATE XVII



EXPLANATION OF PLATE XVIII

Ventral aspect of the head

Fig. 334. *Lyctus planicollis*.

335. *Sphindus americanus*.

336. *Plesiocis cribium*.

337. *Aphodius fimetarius*.

338. *Dichelonyx elongata*.

339. *Pelidnota punctata*.

340. *Strategus julianus*.

341. *Osmoderma eremicola*.

342. *Trox suberosus*.

343. *Pseudolucanus dama*.

344. *Passalus cornuta*.

345. *Parandra brunnea*.

346. *Derobrachus brunneus*.

347. *Glycobius speciosus*.

348. *Tetraopes tetraophthalmus*.

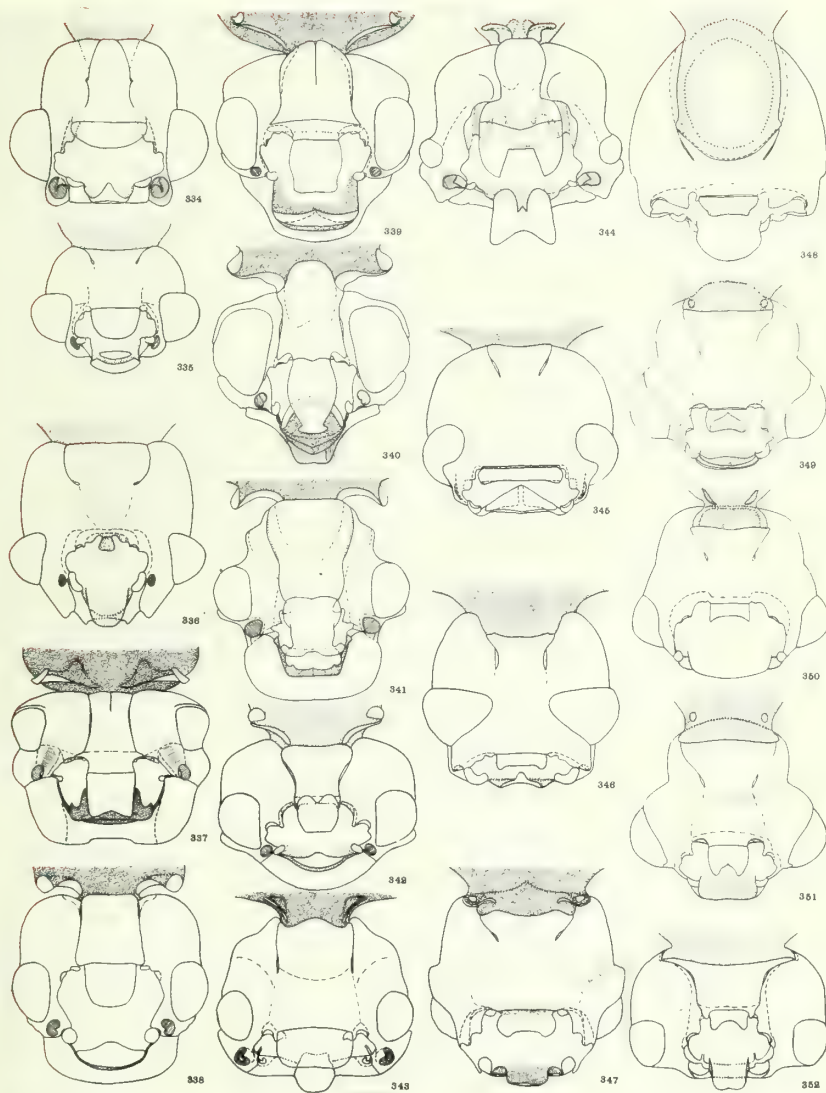
349. *Donacia piscatrix*.

350. *Syneta ferroginea*.

351. *Criocerus asparagi*.

352. *Cryptocephalus quadruplex*.

PLATE XVIII



EXPLANATION OF PLATE XIX

Ventral aspect of the head

Fig. 353. *Chrysochus auratus*.

354. *Leptinotarsa decimlineata*.

355. *Diabrotica 12-punctata*.

356. *Blepharida rhois*.

357. *Anoplitis nervosa*.

358. *Chelymorpha argus*.

359. *Pachymerus arthriticus*.

360. *Eupsalis minuta*.

361. *Eurymycter fasciatus*.

362. *Rhynchites bicolor*.

363. *Attelabus analis*.

364. *Epicaerus imbricatus*.

365. *Scolytus quadrispinosus*.

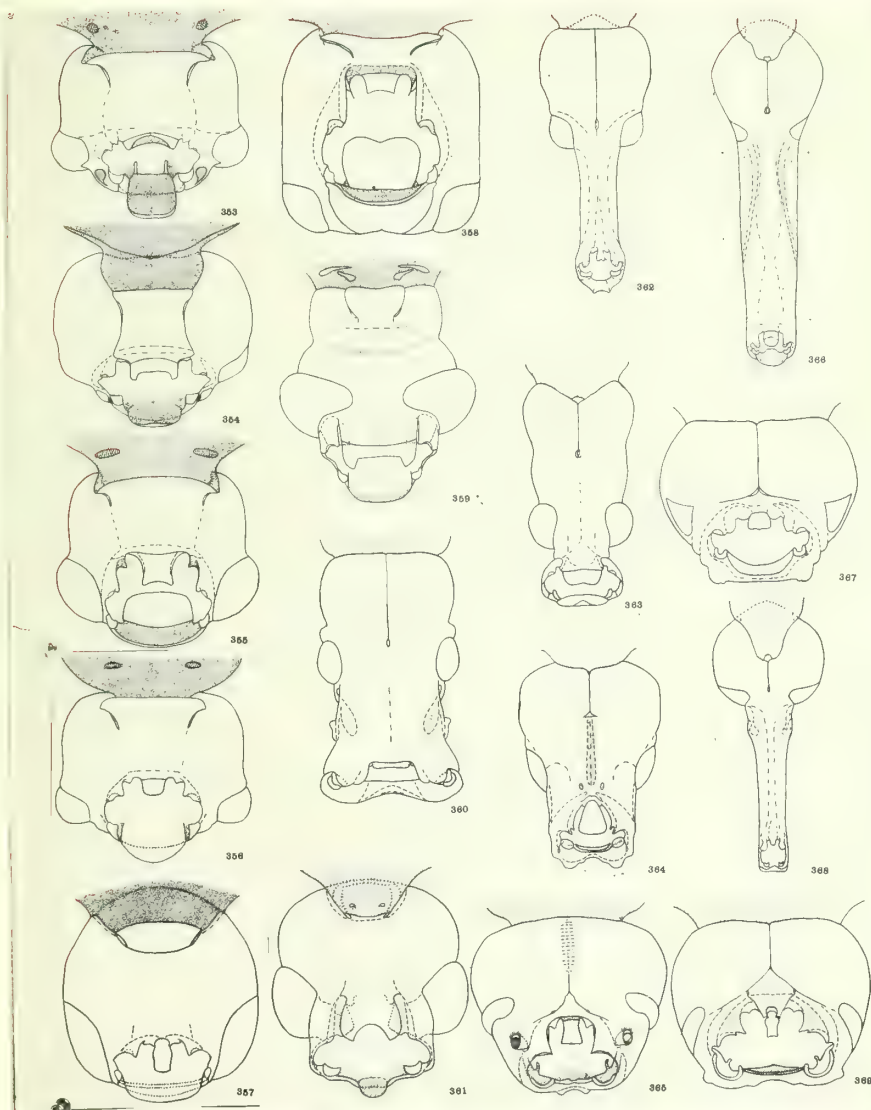
366. *Lixus macer*.

367. *Thecesternus humeralis*.

368. *Sphenophorus aequalis*.

369. *Dendroctonus valens*.

PLATE XIX



EXPLANATION OF PLATE XX

Endoskeleton of the head

Fig. 370. Hypothetical head.

371. *Tetracha carolina*.

372. *Cicindela formosa*.

373. *Calosoma calidum*.

374. *Harpalus erraticus*.

375. *Omophron americanum*.

376. *Peltodytes 12-punctata*.

377. *Cybister fimbriolatus*.

378. *Dineutes assimilis*.

379. *Hydrous triangularis*.

380. *Hydrophilus obtusatus*.

381. *Leptinus testaceus*.

382. *Necrophorus carolina*.

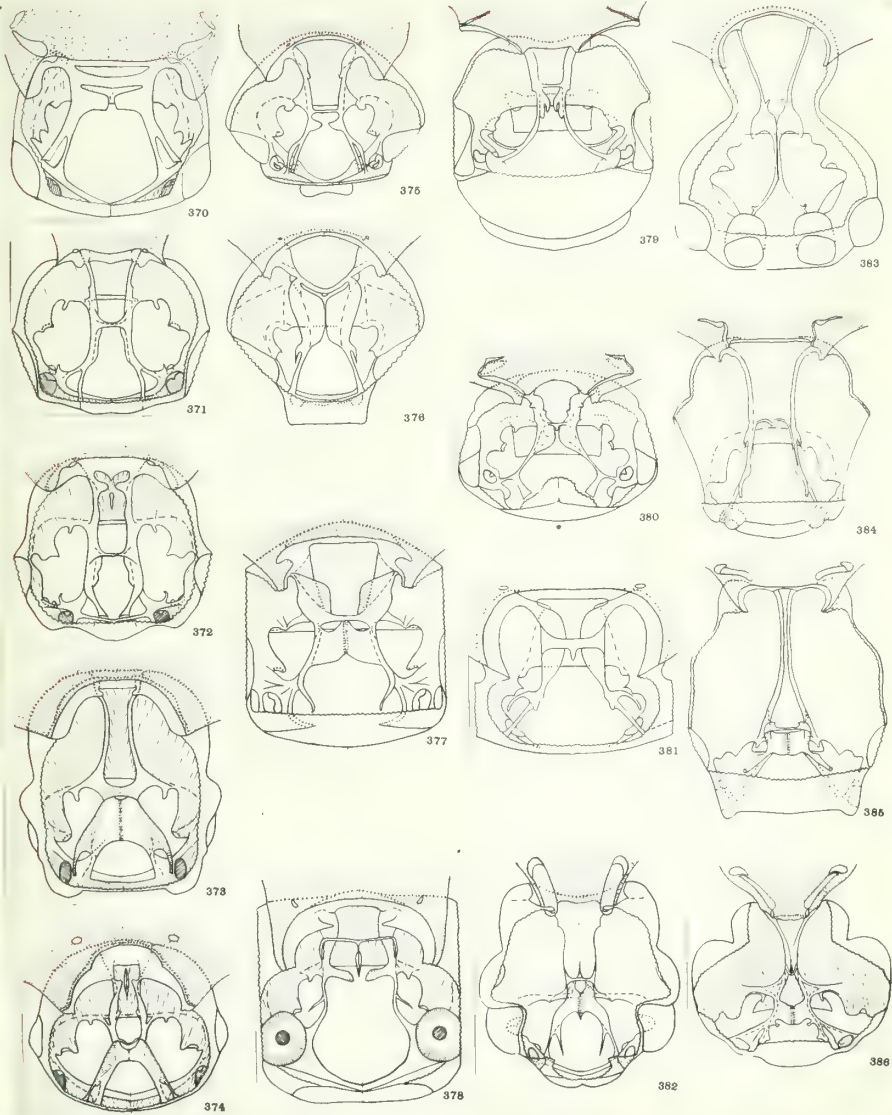
383. *Connophron fossiger*.

384. *Stenus flavicornis*.

385. *Gastrolobium bicolor*.

386. *Creophilus villosus*.

PLATE XX

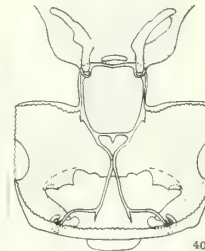
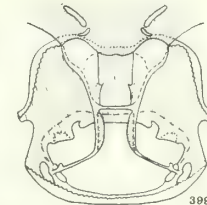
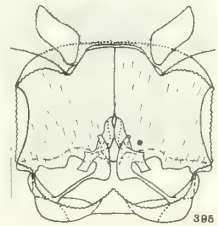
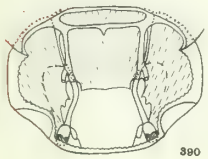
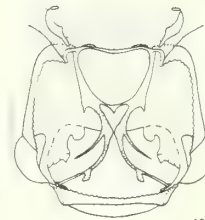
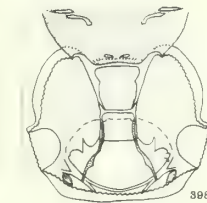
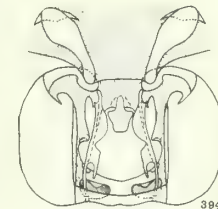
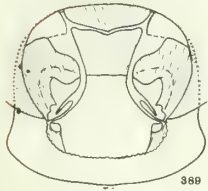
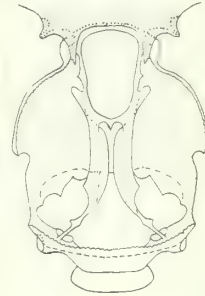
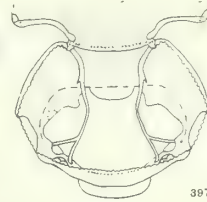
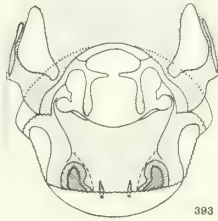
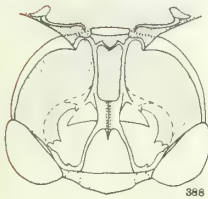
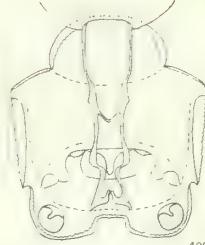
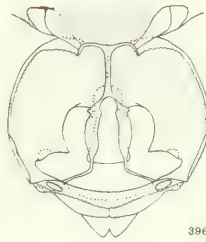
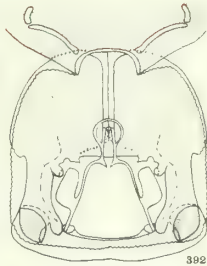
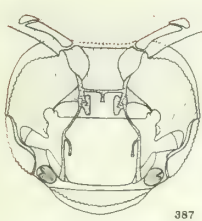


EXPLANATION OF PLATE XXI

Endoskeleton of the head

- Fig. 387. *Tachinus fimbriatus*.
388. *Aleochara lata*.
389. *Limulodes paradoxus*.
390. *Sphaerius politus*.
391. *Scaphidium quadriguttatum*.
392. *Hister merdarius*.
393. *Calopteron terminale*.
394. *Photinus pyralis*.
395. *Phengodes plumosa*.
396. *Chauliognathus pennsylvanicus*.
397. *Collops nigriceps*.
398. *Trichodes nuttali*.
399. *Necrobia rufipes*.
400. *Cupes concolor*.
401. *Cephaloon lepturides*.
402. *Nacerda melanura*.
403. *Tomoxia bidentata*.

PLATE XXI



EXPLANATION OF PLATE XXII

Endoskeleton of the head.

Fig. 404. *Macrosiagon dimidiatum*.

405. *Epicauta marginata*.

406. *Eurystethus debilis*.

407. *Pytho americanus*.

408. *Neopyrochroa flabellata*.

409. *Macratrria murina*.

410. *Notoxus anchora*.

411. *Sandalus niger*.

412. *Alaus oculatus*.

413. *Tharops ruficornis*.

414. *Throscus chevrolati*.

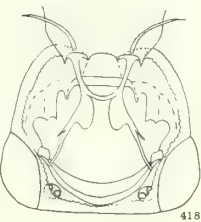
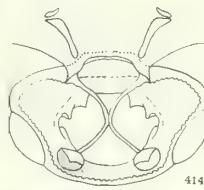
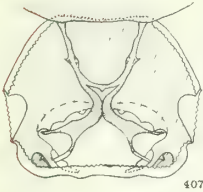
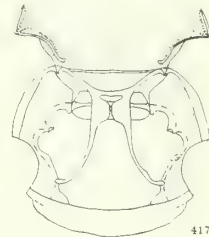
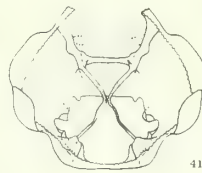
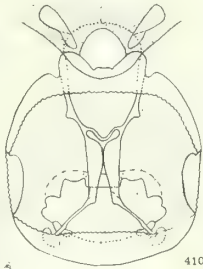
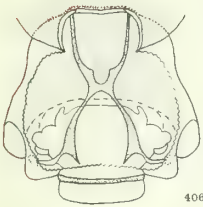
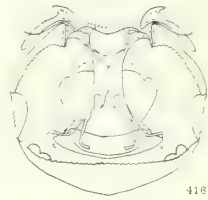
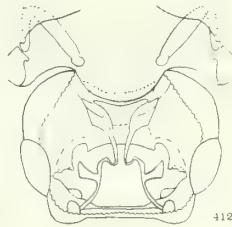
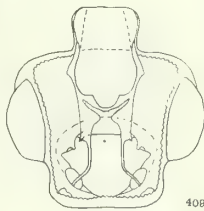
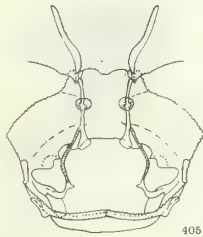
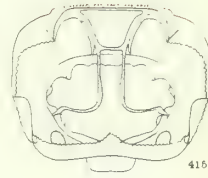
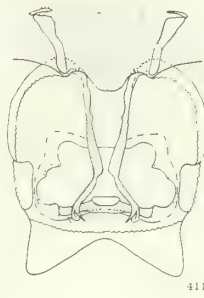
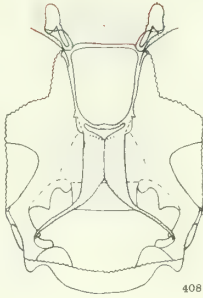
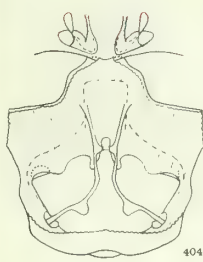
415. *Chalcophora virginienensis*.

416. *Psephenus lecontei*.

417. *Helichus striatus*.

418. *Stenelmis sinuata*.

PLATE XXII

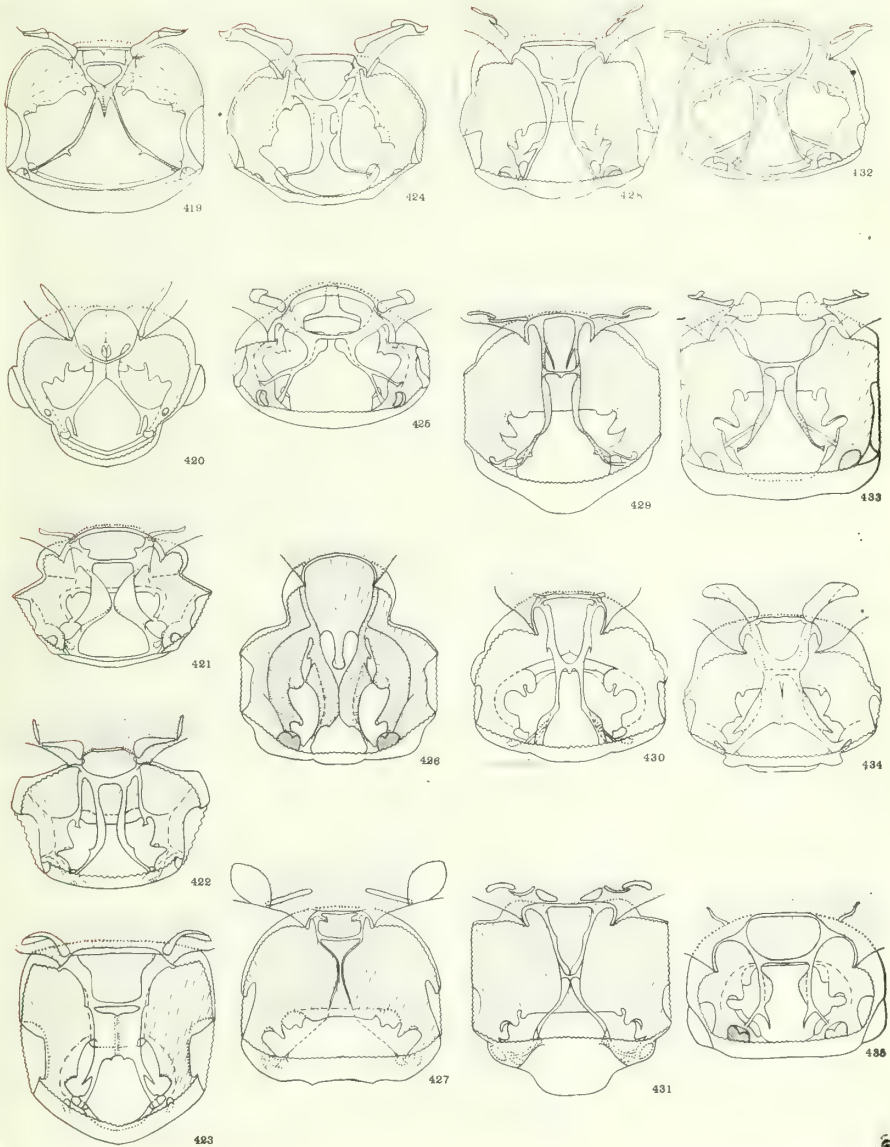


EXPLANATION OF PLATE XXIII

Endoskeleton of the head

- Fig. 419. *Heterocerus undatus*.
420. *Georyssus californicus*.
421. *Eucinetus morio*.
422. *Cyphon ruficollis*.
423. *Dermestes lardarius*.
424. *Byrrhus americanus*.
425. *Nosodendron unicolor*.
426. *Rhysodes americanus*.
427. *Tenebroides sinuata*.
428. *Phenolia grossa*.
429. *Glischrochilus quadriguttatus*.
430. *Phyconomus marinus*.
431. *Cucujus clavipes*.
432. *Languria mozardi*.
433. *Megalodacne fasciatus*.
434. *Derodontus maculatus*.
435. *Anchicera ephippiata*.

PLATE XXIII



EXPLANATION OF PLATE XXIV

Endoskeleton of the head

Fig. 436. *Byturus unicolor*.

437. *Mycetophagus punctatus*.

438. *Philothermus glabriculus*.

439. *Melanophthalma angularis*.

440. *Phymaphora pulchella*.

441. *Endomychus biguttatus*.

442. *Phalacrus politus*.

443. *Hippodamia convergens*.

444. *Adalia bi-punctata*.

445. *Pseudocistela brevis*.

446. *Alobates pennsylvanica*.

447. *Tenebrio molitor*.

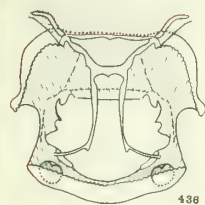
448. *Boros unicolor*.

449. *Arthromacra aenea*.

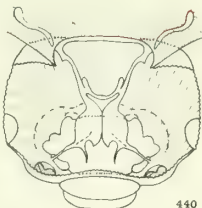
450. *Hyporhagus* sp.

451. *Penthe obliquata*.

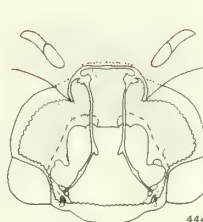
PLATE XXIV



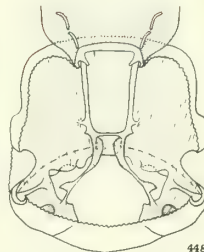
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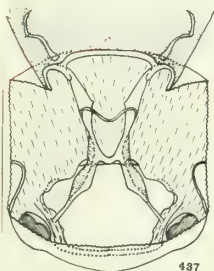
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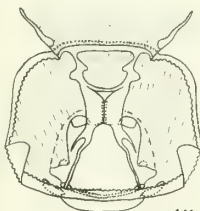
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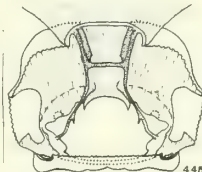
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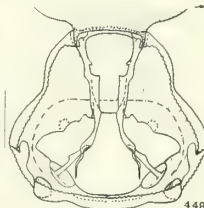
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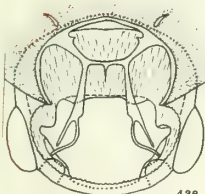
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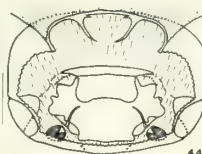
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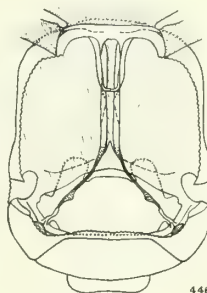
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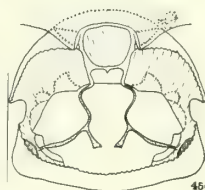
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443



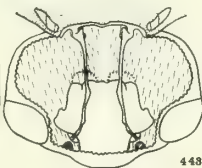
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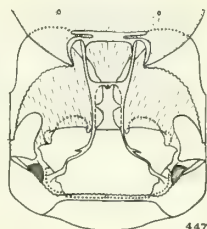
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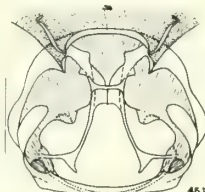
439



448



447



451

EXPLANATION OF PLATE XXV

Endoskeleton of the head

Fig. 452. *Ptinus brunneus*.

453. *Sitodrepa panicea*.

454. *Bostrichus bicornis*.

455. *Lyctus planicollis*.

456. *Sphindus americanus*.

457. *Plesiocis cribrum*.

458. *Aphodius fimetarius*.

459. *Dichelonyx elongata*.

460. *Pelidnota punctata*.

461. *Strategus julianus*.

462. *Osmoderma erimicola*.

463. *Trox suberosus*.

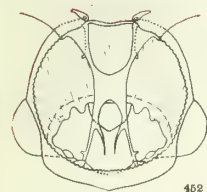
464. *Pseudolucanus dama*.

465. *Passalus cornutus*.

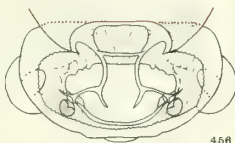
466. *Passalus cornutus*,

lateral aspect, cross-section.

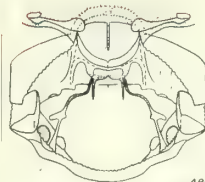
PLATE XXV



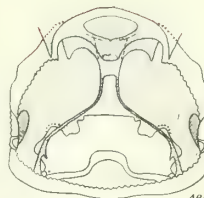
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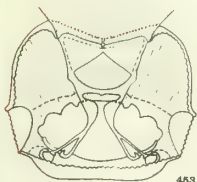
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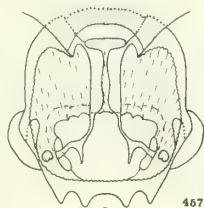
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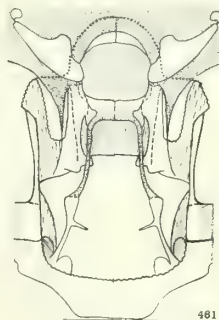
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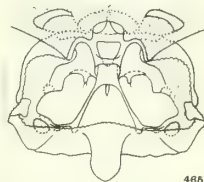
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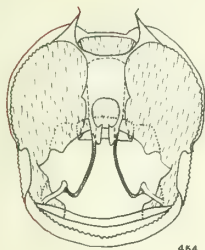
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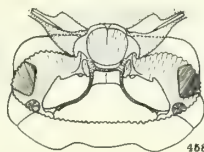
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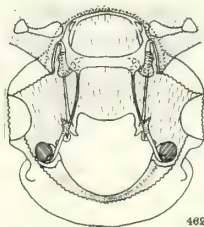
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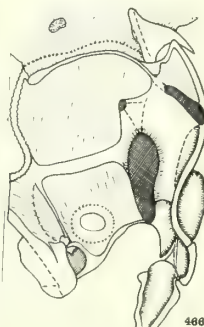
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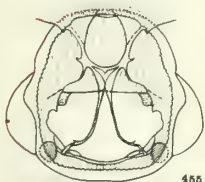
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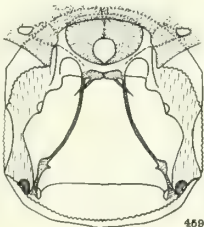
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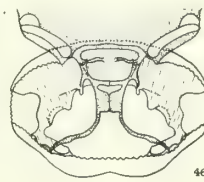
466



465



469



463

EXPLANATION OF PLATE XXVI

Endoskeleton of the head

Fig. 467. *Parandra brunnea*.

468. *Derobrachus brunneus*.

469. *Glycobius speciosus*.

470. *Tetraopes tetraophthalmus*.

471. *Donacia piscatrix*.

472. *Syneta ferruginea*.

473. *Criocerus asparagi*.

474. *Cryptocephalus quadruplex*.

475. *Blepharida rhois*.

476. *Chrysochus auratus*.

477. *Leptinus testaceus*.

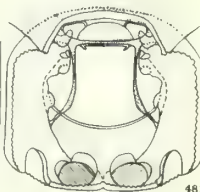
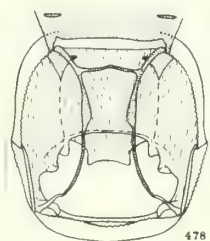
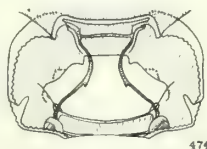
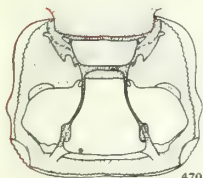
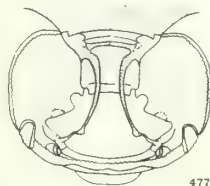
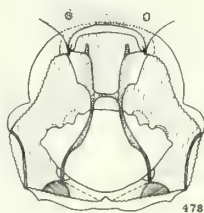
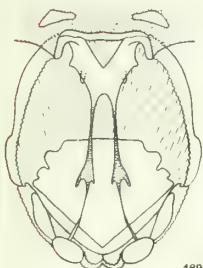
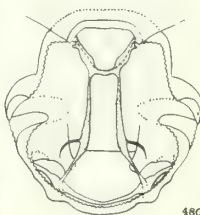
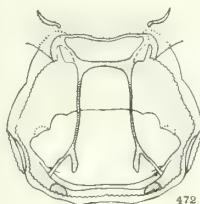
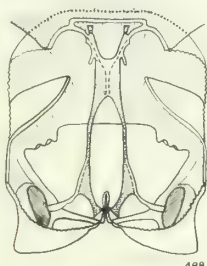
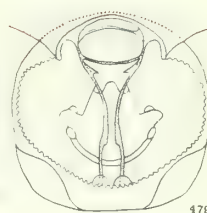
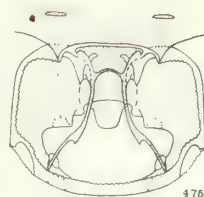
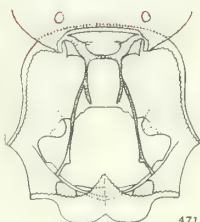
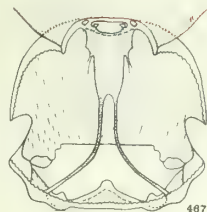
478. *Diabrotica 12-punctata*.

479. *Anoplitis nervosa*.

480. *Pachymerus arthriticus*.

481. *Chelymorpha argus*.

PLATE XXVI

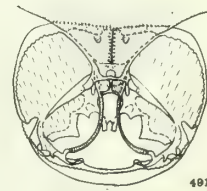
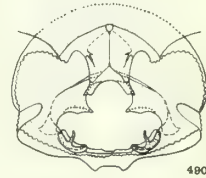
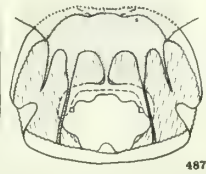
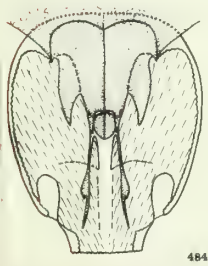
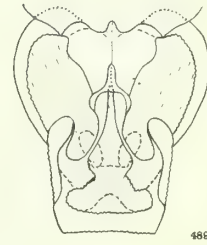
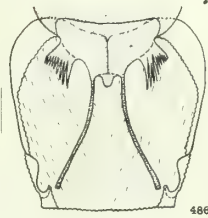
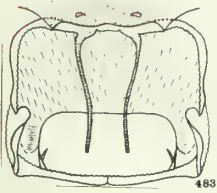
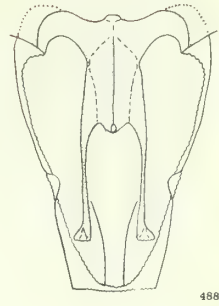
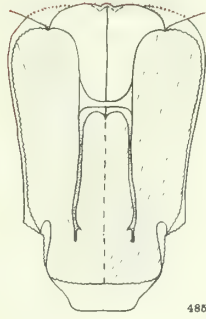
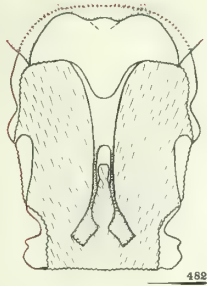


EXPLANATION OF PLATE XXVII

Endoskeleton of the head

- Fig. 482. *Eupsalis minuta*.
483. *Eurymycter fasciatus*.
484. *Rhynchites bicolor*.
485. *Attelabus analis*.
486. *Epicaerus imbricatus*.
487. *Thecesternus humeralis*.
488. *Lixus macer*.
489. *Sphenophorus aequalis*.
490. *Scolytus quadrispinosus*.
491. *Dendroctonus valens*.

PLATE XXVII



VITA

The author of this thesis, Fenner Satterthwaite Stickney, was born in Wilson, North Carolina, August 6, 1892. He attended the public schools of Wilson, until May 1909. The following year he spent on a farm in Beaufort County, North Carolina. During the summer of 1910, he moved to the Hawaiian Islands, and entered in September of that year the McKinley High School of Honolulu, from which he graduated in June 1912. From September 1912 until June 1914, he studied agriculture, including a course in Entomology, at the College, now the University, of Hawaii. In August 1914, he registered in the College of Agriculture of the University of California; he majored in Entomology, and received the degree of Bachelor of Science in Agriculture from that University in May 1916. The year 1916-1917 he spent on a farm in Brunswick County, North Carolina, engaged in practical agriculture. He attended the Summer Session of 1917 at the University of Illinois, specializing in economic Entomology. During the year 1917-18, he was registered in the Graduate School of the University of Illinois, from which he received the degree of Master of Science in Entomology in June 1918. June 1, 1918, he was inducted into the United States Army and ordered to Camp Dodge, Iowa, where he was engaged in sanitary entomological work until August 1918, when he was sent overseas. After six months in France as a member of Sanitary Squad #70, he was returned to the United States, and received his discharge in Honolulu in June 1919. From September 1919 to June 1921 he was a Fellow in Entomology at the University of Illinois. During the summer of 1920 he assisted in extension entomological work at the North Dakota Agricultural College.

EXPLANATION OF PLATE XXVIII

Fig.492. *Amphizoa lecontei*, dorsal aspect.

493. *Amphizoa lecontei*, lateral aspect.

494. *Amphizoa lecontei*, ventral aspect.

495. *Amphizoa lecontei*, endoskeleton.

496. *Pilopius lacustris*, dorsal aspect.

497. *Pilopius lacustris*, lateral aspect.

498. *Pilopius lacustris*, ventral aspect.

499. *Pilopius lacustris*, endoskeleton.

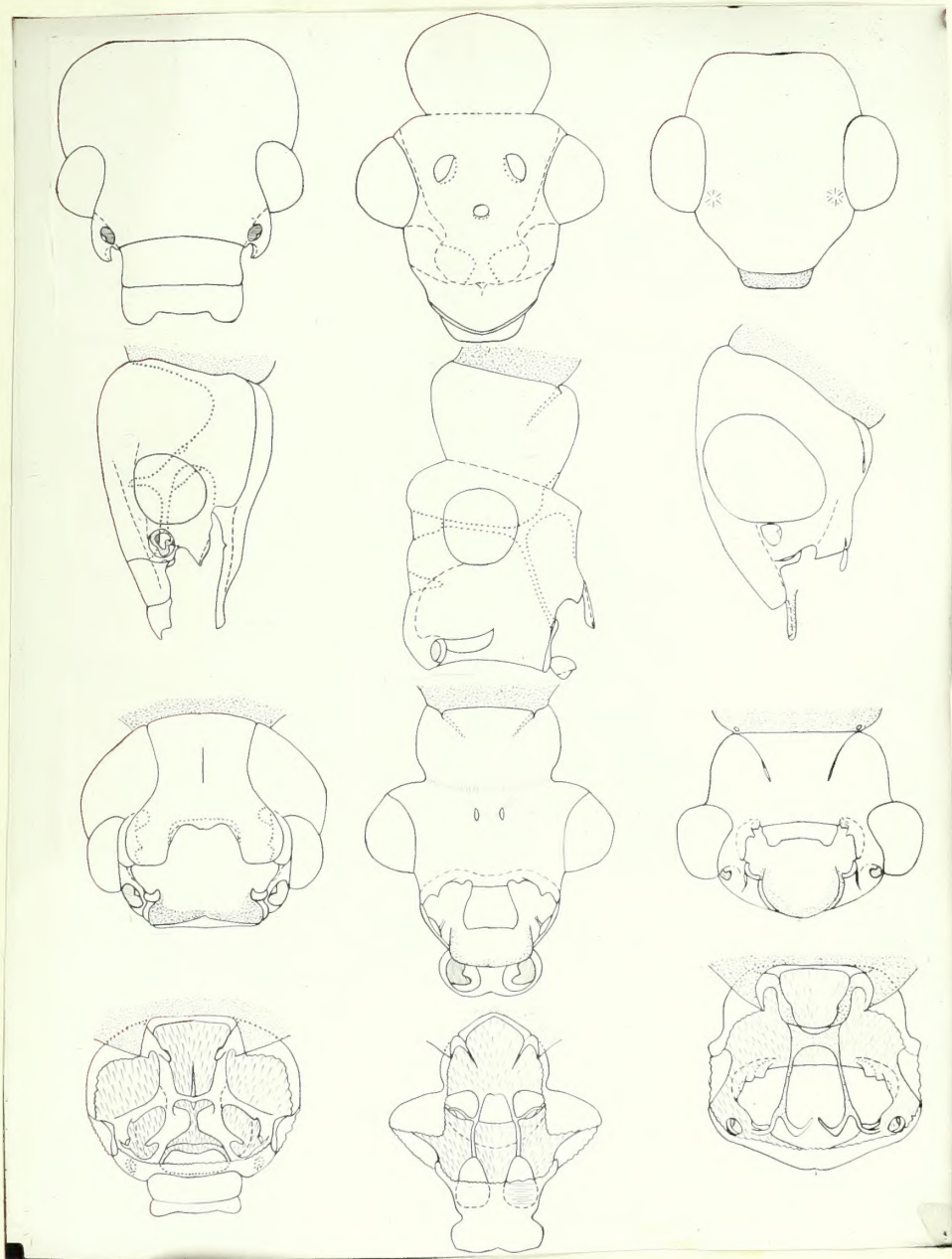
500. *Othnius* sp., dorsal aspect.

501. *Othnius* sp., lateral aspect.

502. *Othnius* sp., ventral aspect.

503. *Othnius* sp., endoskeleton.

PLATE XXVIII



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